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CONTENTS

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A Provisional Check-List and Key to the Mammals of Arkansas (with Annotations)

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Published reports dealing with the mammals of Arkansas are few in number and give only a rather limited coverage of the state as a whole. Only two check-lists of Arkansas mammals have appeared previously. That of Black (1936) covers the northwestern portion of the State while one by Dellinger and Black (1940) is concerned mainly with the Ozark Plateau region of northwestern Arkansas and covers other parts of the State very incompletely. Because the previous lists lack completeness and since changes in nomenclature have to some extent made them obsolete, it has seemed desirable to present a new and revised check-list for the State as a whole. This list is based on the original records along with a large number of new records gathered by the author and his students during the last five years.

Since publication of the earlier check-lists a great many more specimens have been added to the University of Arkansas Zoology Department Collection. Many of these specimens are from areas of the State from which previous collections have not been made. The author has learned of a considerable number of mammal specimens from Arkansas in other collections outside the State through correspondence with individuals and institutions. These specimens are included in the general scope of this paper. Valuable records have been contributed by game wardens and other conservation officials in the State, and records from the literature have been utilized as fully as possible. All of the records now available give a much more accurate distributional picture of the different species found within the State than was previously possible.

A general key to Arkansas mammals is included for the use of high school and college students, game wardens and technical personnel concerned with conservation activities in the State, and other interested persons. The key is based primarily upon study skins and fresh specimens and is intended for both field and laboratory use. Where necessary, tooth and skull characters have been used to make separations in the key and to aid in identifications. Subspecific names in the check-list are largely inferences and are not based on large series of specimens, and too much importance should not be attached to them. It is the author's hope that additional records of some of the less well-known species found within the political confines of Arkansas may result from use of the key by various individuals in the State.

The present list includes several new species and subspecies not mentioned in previous reports. Some have been recorded recently while others were

[1] This study was aided by grants from the Sigma Xi-RESA Research Fund and the Research Fund of the College of Arts and Sciences, University of Arkansas.

reported earlier in the literature but were not included in the previous checklists. Some subspecies reported here are the result of taxonomic revisions made in the last few years. The author is not a firm believer in trinomial nomenclature but is essentially in agreement with the views of Burt (1954), Hubbell (1954), and others with a similar approach to the subspecies concept. Subspecific names have been used chiefly to indicate the amount of variation within certain species found in the State and to make this paper more useful to those more taxonomically inclined individuals who still persist in naming each variant population. For the sake of uniformity, subspecific names have been assigned to all species where known, although it is not considered that each of these is an incipient species. Specimens have been assigned to one

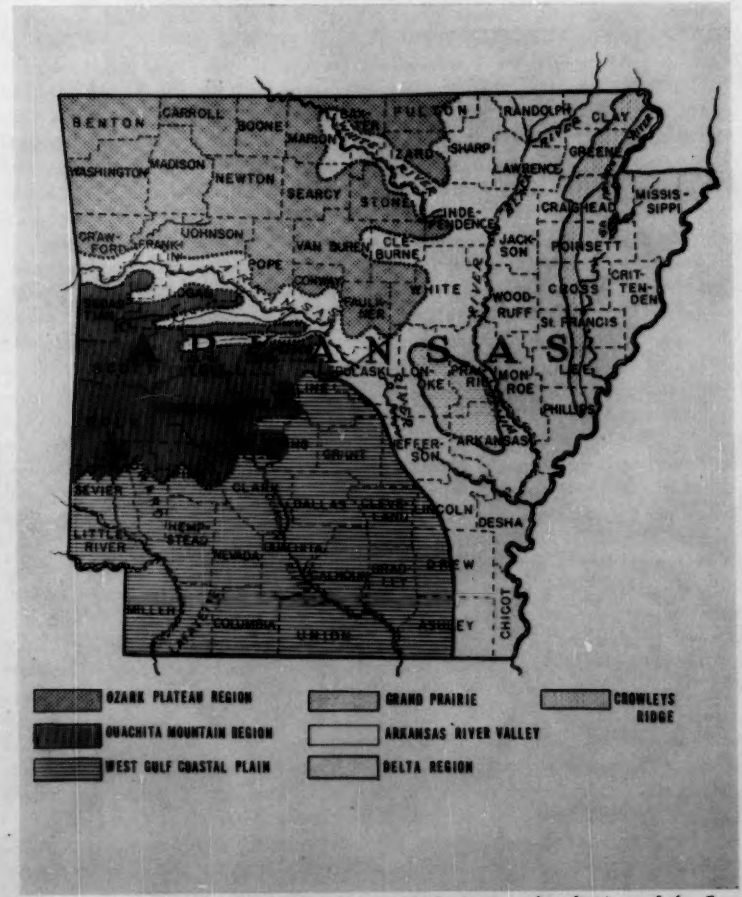


FIG. 1.—County map of Arkansas showing principal physiographic divisions of the State.

or another subspecies both on the basis of comparison of specimens with type descriptions and by making inferences from geographic ranges given in the literature. In general the arrangement of species and subspecies follows that of Miller and Kellogg (1955), but in a few cases their arrangement has been modified with respect to genera where Simpson (1945) and other authorities are believed to be more nearly correct in their arrangement.

Those persons interested in collecting methods and preparation of mammals as study specimens should consult the publication by Anderson (1948). Other publications dealing with this same subject are Booth (1949), Burt (1946), and Gunderson and Beer (1953).

The following information is not intended to be a complete account of the mammal fauna of Arkansas, but is expected to fulfill a definite temporary need for more knowledge concerning State mammals until a more complete account, now in preparation by the writer, can be published. Much additional data concerning Arkansas mammals is needed before this latter work can be finished, and the present paper merely serves to bridge some of the numerous gaps which now exist in the recorded accounts of this fauna.

Arkansas is in a very interesting geographic area in which the range of some western and southwestern forms apparently reach their eastern limits and the ranges of some eastern forms apparently reach their western limits. Likewise, some northern and southern forms seem to reach their southern and northern limits respectively within the political confines of the State. Further studies of Arkansas mammals are greatly needed. It would, for example, be desirable to investigate more fully the roles which vegetation, soil type, climate, and topography play in determining species distribution within the State. More work concerning mammal population densities, behavior, and ecological and physiological factors affecting speciation and variation in mammal populations is also needed.

Distributional information contained in this paper is based upon Arkansas specimens in a number of collections besides that of the University of Arkansas Zoology Department. A list of abbreviations used in this account with an explanation of their meaning is as follows:

AJH—Collection of A. J. Hoiberg, El Dorado, Arkansas
ASM—Collection of A. S. Morgan, Winfield, West Virginia
AMNH—American Museum of Natural History
BS—Biological Surveys Sollection of the Fish and Wildlife Service
CNHM—Chicago Natural History Museum
IU—University of Illinois, Museum of Natural History
KU—University of Kansas, Museum of Natural History
LY—Collection of Lyndal York, Fort Smith, Arkansas
MCZ—Museum of Comparative Zoology, Harvard College
MNS—Museum of Natural Science, Louisiana State University
MVZ—Museum of Vertebrate Zoology, University of California
MZM—Museum of Zoology, University of Michigan.
ODZ—Oklahoma A. and M. College, Department of Zoology collection
UADZ—University of Arkansas Department of Zoology collection
USNM—United States National Museum

In addition to the above named institutions, Mr. T. H. Holder of the Arkansas Game and Fish Commission has been of much assistance in making available distributional records of certain game and furbearing species on file in his office. Many state game wardens and refuge keepers throughout the State have provided records of those species with

which they are familiar, and occasional records have been contributed by the author's students and by other individuals.

I wish to express appreciation to all of those individuals and institutions who have provided me with information concerning specimens in their collections or who have furnished information used in this paper. Space does not permit enumeration of each of them by name.

List of Species

Family DIDELPHIDAE

DIDELPHIS MARSUPIALIS VIRGINIANA Kerr—Virginia Opossum

The opossum is statewide in distribution and is common in nearly all localities. It appears to be most common in heavily timbered bottomlands of eastern Arkansas and in the mountainous regions of the State. It is least common in the more open bottomland areas in the Arkansas River Valley and in the prairie areas of the State. Although heavily trapped, ranking first in numbers trapped in the State, it continues to be abundant. Melanistic and albinistic specimens occur with a fair degree of regularity, while an occasional specimen appearing among skins purchased by fur buyers is in the cinnamon color phase.

Specimens examined.—UADZ, total 11. BOONE Co.: 3 miles S Harrison (1); GARLAND Co.: Avant (1); RANDOLPH Co.: Dalton (2); WASHINGTON Co.: (1), Fayetteville (5), 1 mile N Springdale (1).

Additional specimens.—total 25. ARKANSAS Co.: Stuttgart (1-USNM); BOONE Co.: (7-MVZ), Bergman (8-MVZ); CRAWFORD Co.: (1-KU); SEBASTIAN Co.: (1-MZM); WASHINGTON Co.: (2-BS), (3-KU), (1-MCZ), (1-MZM).

Other records.—BAXTER Co.: Mountain Home (1)—Dellinger and Black (1940); BENTON Co.: Eden's Bluff (1)—Dellinger and Black (1940); CRAWFORD Co.: Mountainburg (1)—Black (1936); WASHINGTON Co.: Winslow (3)—Black (1936), Elkins (1), Springdale (1), Sulphur City (1)—Dellinger and Black (1940).

Family SORICIDAE

BLARINA BREVICAUDA CAROLINENSIS (Bachman)—Carolina Short-tailed Shrew

This is the most common shrew found in Arkansas. It is widely distributed in suitable habitat throughout the State. Many people are in the habit of calling this species a "baby mole".

Specimens examined.—UADZ, total 17. JEFFERSON Co.: Pine Bluff (1); POLK Co.: Eagleton (1), Mena (4); SEBASTIAN Co.: Fort Smith (2); UNION Co.: Eldorado (3); WASHINGTON Co.: Fayetteville (3), West Fork (1), Winslow (3).

Additional specimens.—total 12. CRAIGHEAD Co.: Lake City, (3-BS); DREW Co.: Monticello (1-CNHM); GARLAND Co.: Hot Springs (1-CNHM); PIKE Co.: Delight (1-BS), (4-MCZ); WASHINGTON Co.: (1-KU); WHITE Co.: Beebe (1-BS).

Other records.—FULTON Co.: Mammoth Springs (1)—Dellinger and Black (1940); INDEPENDENCE Co.: Batesville (1)—W. L. Henning (*in. litt.*); POPE Co.: Moreland (1), Russellville (1)—E. B. Holmes (*in. litt.*); WASHINGTON Co.: Fayetteville (6), University Farm (2)—Dellinger and Black (1940); INDEPENDENCE Co.: Batesville (1)—W. L. Henning (*in litt.*); POPE Co.: Moreland (1), Russellville (1)—E. B. Holmes (*in litt.*); WASHINGTON Co.: Fayetteville (6), University Farm (2)—Dellinger and Black (1940), Winslow (1)—Black (1936).

CRYPTOTIS PARVA PARVA (Say)—Little Short-tailed Shrew

This is the smallest mammal found in the State. Undoubtedly it is state wide in distribution but has been poorly collected. There is some indication

of cyclic fluctuation in numbers of this species. During some years it seems to be extremely numerous in certain localities and then virtually disappears for long periods of time. One of these periods of abundance apparently occurred in 1949. Since then it has not occurred in exceptionally large numbers in the State.

Specimens examined.—UADZ, total 30. ARKANSAS Co.: Big Island Chute (4); JEFFERSON Co.: Pine Bluff (1) PIKE Co.: Murfreesboro (1); POLK Co.: Mena (1); SEBASTIAN Co.: Fort Smith (1); UNION Co.: Eldorado (1); WASHINGTON Co.: Farmington (1), Fayetteville (19), Lake Wedington area (1).

Additional specimens.—total 12. DREW Co.: Monticello, (1-CNHM); WASHINGTON Co.: Winslow (11-KU).

Other records.—ARKANSAS Co.: St. Charles (20)—Dellinger and Black (1940); POLK Co.: Mena (2)—R. B. Loomis (*in litt.*); WASHINGTON Co.: Fayetteville (1)—Dellinger and Black (1940).

NOTIOSOREX CRAWFORDI CRAWFORDI (Coues) Crawford Shrew

Known only from Natural Dam, Crawford County (Sealander, 1952). This rare shrew is probably present only along the extreme western edge of the State, and intensive collecting will be necessary to secure more specimens. The Arkansas specimen is deposited in the United States National Museum.

Specimens examined.—USNM, total 1. CRAWFORD Co.: Natural Dam (1-USNM).

Family TALPIDAE

SCALOPUS AQUATICUS MACHRINOIDES Jackson—Missouri Valley Mole

SCALOPUS AQUATICUS PULCHER Jackson—Arkansas Mole

Moles are common throughout the rich bottomlands and in the more open areas of the State. They are not common in heavily wooded uplands. Most of the moles in the State are referable to the race *pulcher* which intergrades with the race *machrinoides* in the northern tier of counties. Specimens from Washington, Stone, Independence, and Clay counties are somewhat intermediate between the two races but in general characteristics seem to be most similar to the race *machrinoides*. Occasional reports of golden moles are received from various parts of the State. One specimen exhibiting this color variation (not true albinism) from Washington County is in the University of Arkansas mammal collection.

Specimens examined.—UADZ, total 17. GARLAND Co.: Buckville (1); MADISON Co.: Alabam (1); WASHINGTON Co.: Fayetteville (13), Goshen (1), Winslow (1).

Additional specimens.—total 47. ASHLEY Co.: Wilmot (1-BS); CLAY Co.: Greenway (7-BS), (1-CNHM); CRAIGHEAD Co.: Lake City (1-BS); OUACHITA Co.: Camden (1-BS); PIKE Co.: Delight (15-BS), (4-MCZ); SEBASTIAN Co.: Fort Smith (1-BS); STONE Co.: Marcella (2-CNHM); WASHINGTON Co.: Fayetteville (1-CNHM), (3-KU), Winslow (9-KU), (1-USNM).

Other records.—INDEPENDENCE Co.: Batesville (12)—W. L. Henning (*in litt.*).

Family VESPERTILIONIDAE

MYOTIS LUCIFUGUS LUCIFUGUS (Le Conte)—Little Brown Bat

The little brown bat is probably state wide in distribution, at least during the summer months. It is typically a cave bat (Sealander and Young, 1955)

and probably occurs in small numbers throughout the mountainous regions of the State where caves are numerous. In other areas it may occur in dwelling places. This species has been taken during winter in Arkansas caves in a dormant condition. At present this bat is definitely known from only a few counties in Arkansas. According to B. P. Glass (*in. litt.*) it has been taken in Delaware County, Oklahoma which lies adjacent to Benton County in northwestern Arkansas.

Specimens examined.—UAZD, total 2; KU, total 7. GARLAND CO.: 12 miles NW Hot Springs (2); PRAIRIE CO.: Devall's Bluff (7-KU).

Additional specimens.—total 5. INDEPENDENCE CO.: Forshee's Cave (1-CNHM); SEBASTIAN CO.: Fort Smith (1-USNM); STONE CO.: Fifty-Six (3-MVZ).

MYOTIS AUSTRORIPARIUS MUMFORDI Rice—Mississippi Bat

This race of the Mississippi bat which occurs in Indiana, Illinois, and Arkansas has recently been described by Rice (1955). It was first collected in Arkansas on November 27, 1952 (Davis, Lidicker, and Sealander, 1955). In general appearance this bat closely resembles the little brown bat. This species is still known only from one locality in Arkansas.

Specimens examined.—UADZ, total 5. GARLAND CO.: 12 miles NW Hot Springs (5).

MYOTIS GRISESCENS Howell—Gray Bat

The gray bat is a common cave bat of northern Arkansas (Sealander and Young, 1955). In winter it occurs in large numbers in several of the numerous caves in the region and maintains breeding colonies in some caves during the spring and early summer months. During winter it seems to disappear or become scarce in many of the caves where it is found. The writer and Dr. Howard Young discovered that during this time they wedge themselves far back into deep crevices in the cave walls. In late spring they emerge and gather in large clusters just prior to the breeding season in late April and May.

This bat was first reported from Arkansas by Miller and Allen (1928) who listed one specimen from Carroll County. It has been reported from several counties since but has not been taken south of the Arkansas River.

Specimens examined.—UADZ, total 33. BENTON CO.: Crystal Cave-Bentonville (2), Logan Cave-Siloam Springs (8), Bat Cave-War Eagle (4); INDEPENDENCE CO.: Bone Cave-Batesville (1); MADISON CO.: Denney Cave-Alabam (5); WASHINGTON CO.: Bat Cave-Springdale (11), Quarry Cave- Johnson (2).

Additional specimens.—total 363. BENTON CO.: Cave Spring Cave-Cave Spring (3-AMNH), (52-KU), (8-MCZ), Bentonville, (168-KU), (18-MVZ), Logan Cave-Siloam Springs (1-IU), Bat Cave-War Eagle (15-KU); CARROLL CO.: Osage River (1-MCZ); INDEPENDENCE CO.: Bone Cave-Batesville (30-CNHM); MADISON CO.: Denney Cave-Alabam (3-AMNH), (45-KU); WASHINGTON CO.: Bat Cave-Springdale (16-CNHM).

Other records.—BENTON CO.: Bella Vista Cave-Bella Vista (2), Crystal Cave-Bentonville (12)—Dellinger and Black (1940); STONE CO.: Marcella (several)—C. C. Sanborn (*in litt.*).

MYOTIS KEENII SEPTENTRIONALIS (Trouessart)—Eastern Long-eared Bat

This is not a common species in Arkansas but probably occurs in small numbers in most of the northern two-thirds of the State. It remains dormant

in caves or old mine shafts during winter, but never in large numbers. Miller and Allen (1928) listed a specimen from Delight, Pike County, and Dellinger and Black (1940) reported it from Benton County. It is now known from a few more counties as well.

Specimens examined—UADZ, total 9. BENTON CO.: Crystal Cave-Bentonville (2), Bat Cave-War Eagle (1); GARLAND CO.: 12 miles NW Hot Springs (3); WASHINGTON CO.: Devil's Den Cave-Winslow (3).

Additional specimens.—total 2. BENTON CO.: Crystal Cave-Bentonville (1-MVZ); INDEPENDENCE CO.: Cushman Cave-Cushman (1-CNHM).

Other records.—PIKE CO.: Delight (1)—Miller and Allen (1928).

MYOTIS SODALIS Miller and G. M. Allen—Indiana Bat

The social or Indiana bat is common in at least the northern one-third of the State. Over two hundred individuals of this species have been banded in Arkansas (Sealander and Young, 1955). It was first reported by Miller and Allen (1928) and subsequently Black (1934, 1936) reported it from Benton and Madison counties. It is now known from several other counties as well.

Specimens examined.—UADZ, IU, ODZ, total 30. BENTON CO.: Bat Cave-War Eagle (13), (2-IU); MADISON CO.: Denney Cave-Alabam (3), (2-ODZ); SEARCY CO.: Great Hurricane Cave-Western Grove (2), Gilbert (1); WASHINGTON CO.: Nichol's Cave-Hicks (6), Devil's Den Cave-Winslow (1).

Additional specimens.—total 112. BENTON CO.: Bat Cave-War Eagle, (51-KU); CLAY CO.: Greenway, (2-CNHM); INDEPENDENCE CO.: Cushman Cave-Cushman (8-CNHM); IZARD CO.: Calico Rock (1-MZM); MADISON CO.: Denney Cave-Alabam (3-KU); STONE CO.: Fifty-Six (47-MVZ).

Other records.—BAXTER CO.: Twigly Cave-Midway (1)—R. L. Jordan (*in. litt.*)

PIPISTRELLUS SUBFLAVUS SUBFLAVUS (F. Cuvier)—Southern Pipistrelle

Without doubt this is the commonest species of bat in the State. It winters in large numbers in some of the larger caves throughout the Ozarks, and one or two of these bats may be found hanging dormant in nearly any small cave during the winter months. Although an occasional individual may be found in moist caves during the summer, the majority leave the caves by late April or May (Sealander and Young, 1955). Speicmens found in caves after mid-April are almost invariably males. This species is almost always solitary in caves. On a few occasions the writer has found as many as three or four individuals in a cluster.

Color dimorphism appears to be common in this species. Variations in color from very pale yellowish-buff to brownish-yellow are common. Occasional light individuals occur in populations of the northern race *obscurus* as do dark individuals in the southern race *subflavus*. Whether the northern race which is based largely on color is valid may depend upon further taxonomic study of the species.

Specimens examined.—UADZ, IU, total 59. BENTON CO.: Indian Cave-Bella Vista (1), Crystal Cave-Bentonville (1), Cave Spring Cave-Cave Spring (1), Monte Ne Cave-Monte Ne (1), Logan Cave-Siloam Springs (1), Bat Cave-War Eagle (12); BRADLEY CO.: Stillions (1); FRANKLIN CO.: Cass (1); INDEPENDENCE CO.: Bone Cave-Batesville (1); NEWTON CO.: Lost Valley Cave-Ponca (5), Big Cave-Erbie (3); OUACHITA CO.: Smackover (1); SEARCY CO.: Great Hurricane Cave-Western Grove (2); WASHINGTON CO.: Granny Dean Cave-Black Oak (1), Fincher Cave-Black Oak

(2), Corkscrew Cave-Fayetteville (2), Nichol's Cave-Hicks (11), (1-IU); Quarry Cave-Johnson (2), Devil's Den Cave-Winslow (7), Devil's Icebox Cave-Winslow (2).

Additional specimens.—total 332 plus. BENTON, MADISON, AND WASHINGTON Cos.: (300 plus-KU); BENTON Co.: Gregory Cave-Decatur (2-MVZ), Gravette (3-MVZ), Bat Cave-War Eagle (4-MVZ); INDEPENDENCE Co.: Forshee's Cave (3-CNHM), Bone Cave-Batesville (1-CNHM), Cushman Cave-Cushman (1-CNHM); MADISON Co.: Pettigrew (3-BS); NEWTON Co.: Jasper (4-KU); SEBASTIAN Co.: Fort Smith (2-BS); WASHINGTON Co.: Granny Dean Cave-Black Oak (4-CNHM), Fincher Cave-Black Oak (1-CNHM), Fayetteville (3-BS), Springdale (1-CNHM).

Other records.—BAXTER Co.: Twigly Cave-Midway (1)—R. L. Jordan (*pers. comm.*); BENTON Co.: Cave Spring Cave-Cave Spring (25)—P. Callahan (*pers. comm.*), Logan Cave-Siloam Springs (57) banded—W. H. Davis (*in litt.*); FRANKLIN Co.: Ozark (4)—Black (1936); GARLAND Co.: 12 miles NW Hot Springs (8)—F. B. Truett (*pers. comm.*); INDEPENDENCE Co.: Bone Cave-Batesville (3)—W. L. Henning (*in litt.*); MADISON Co.: Denny Cave-Alabam (numerous), many banded—Black (1936), Sealander and Young (1955); SEARCY Co.: Bear Creek Cave-Gilbert and Great Hurricane Cave-Western Grove (observed)—R. L. Jordan (*pers. comm.*); SCOTT Co.: Treasure Cave-Waldron (reported)—Black (1936); STONE Co.: Marcella (reported)—C. C. Sanborn (*in. litt.*); WASHINGTON Co.: Basset Cave-Hicks (5)—personal observation, Dexter Cave-Sulphur City (2)—personal observation; Delap Caves-Prairie Grove (13)—personal observation; White River Cave-Springdale (7)—personal observation.

EPTESICUS FUSCUS FUSCUS (Palisot de Beauvois)—Big Brown Bat

The big brown bat is apparently common in the State although it has never been taken in large numbers. It is probably statewide in distribution but has not been reported from most of eastern Arkansas. This is a very hardy species and probably seldom enters caves in this region except during the severest weather. Rysgaard (1942), who studied this bat in Minnesota, found that it often did not enter caves there until late November or December. It is seldom that more than one or two *Eptesicus* are found in Arkansas caves, although they were reported in large numbers from Devil's Den Cave, Washington County, in October 1935 (Dellinger and Black, 1940). The writer has banded bats in this cave over a period of five years and has not yet observed a single individual of this species there.

Specimens examined.—UADZ, total 7. BAXTER Co.: Twigly Cave-Midway (1); BENTON Co.: Crystal Cave Bentonville (2); MADISON Co.: Denney Cave-Alabam (1), Mitchell Cave-Alabam (1); SEARCY Co.: Bear Creek Cave-Gilbert (1); WASHINGTON Co.: Fayetteville (1).

Additional specimens.—total 13. CARROLL Co.: Osage River (1-MCZ); CLAY Co.: Greenway (1-CNHM); INDEPENDENCE Co.: Bone Cave-Batesville (2-CNHM), (2)—W. L. Henning (*in. litt.*); PIKE Co.: Delight (1-BS); SALINE Co.: (1-MZM); SEBASTIAN Co.: Fort Smith (3-USNM); SCOTT Co.: mouth of Poteau River (1-USNM); STONE Co.: Marcella (1-CNHM).

Other records.—BENTON Co.: Bat Cave-War Eagle (1)—Black (1936); FRANKLIN Co.: Bat Cave-Ozark (1)—Black (1936); MADISON Co.: Denney Cave-Alabam (1)—Black (1936); WASHINGTON Co.: Devil's Den Cave-Winslow (large numbers)—Dellinger and Black (1940), Winslow (3)—Black (1936).

LASIURUS BOREALIS BOREALIS (Miller)—Northern Red Bat
LASIURUS BOREALIS SEMINOLUS (Rhoads)—Seminole Red Bat

The northern red bat seems to be quite common and well distributed throughout the State. Most bats that are shot in flight and picked up while

carrying young in early summer are of this species. This bat has seldom been recorded from caves, seeming to prefer trees. Apparently this species winters in Arkansas and Missouri although it migrates southward in winter from more northern states. W. H. Davis (*in. litt.*) mentions shooting a red bat on February 4, 1954 in Stone County, Missouri which lies adjacent to Arkansas' northern border. The writer has observed this bat in flight in Washington County during the latter part of January. The race *seminolus* thus far has been taken only from near Newport Landing on the Ouachita River, near Smackover, Ouachita County (Sealander and Hoiberg, 1954). This race is considered a separate species by some authorities. The possibility also exists that it may be only a color phase of the race *borealis*.

Specimens examined.—UADZ, total 10. BRADLEY CO.: 20 miles SW Warren (3); GARLAND CO.: 5 miles NW Mt. Taber (1); JEFFERSON CO.: Pine Bluff (1); OUACHITA CO.: Newport Landing-Smackover (1); SEBASTIAN CO.: Fort Smith (1); UNION CO.: El Dorado (2); WASHINGTON CO.: Fayetteville (1), Winslow (1).

Additional specimens.—total 27. COLUMBIA CO.: McNeil (1-AJH); CLAY CO.: Greenway (5-CNHM); PIKE CO.: Delight (1-BS); PULASKI CO.: Little Rock (2-MNS); SEBASTIAN CO.: Fort Smith (2-USNM); WASHINGTON CO.: Winslow (18-KU).

Other records.—CRAWFORD CO.: Mountainburg (observed)—Black (1936); WASHINGTON CO.: Fayetteville (observed)—Black (1936), West Fork (1)—M. A. Jacobs (*pers. comm.*).

LASIURUS CINEREUS CINEREUS (Palisot de Beauvois)—Hoary Bat

It is probable that this species has a limited distribution over most of the State although only six specimens have so far been reported (Sealander, 1954).

Specimens examined.—LY, total 1. SEBASTIAN CO.: Fort Smith, (1-LY) (note: this specimen was accidentally destroyed by Lyndal York after it had been examined by the writer).

Additional specimens.—total 2. GARLAND CO.: Hot Springs (2)—in Hot Springs National Park Museum collection, cf. Gregg (1937).

Other records.—PULASKI CO.: Little Rock (3)—Dellinger and Black (1940); WASHINGTON CO.: Winslow (reported)—Dellinger and Black (1940).

NYCTICEIUS HUMERALIS HUMERALIS (Rafinesque)—Evening Bat

This bat probably occurs in limited numbers over most of the State, although very few specimens have been collected.

Specimens examined.—UADZ, total 1. BRADLEY CO.: Stillions (1).

Additional specimens.—total 12. BAXTER CO.: Cotter (1-BS); CARROLL CO.: Osage River (3-MCZ); DESHA CO.: McGehee (3-BS); SEBASTIAN CO.: Ft. Smith (5-USNM).

CORYNORHINUS TOWNSENDII INGENS Handley—Western Lump-nosed Bat

Until 1950 only a single specimen of this species was known from the State (Black, 1936). On October 15, 1950 and December 4, 1950 the writer collected additional specimens from Hewlitt cave, 12 miles west of Fayetteville, Washington County. Several more specimens were obtained in Devil's Icebox cave, Washington County, in 1951 and 1952, and a few individuals were banded (Sealander, 1951a; Sealander and Young, 1955). Specimens have been collected from three other caves in Washington, Madison and Craw-

ford counties since this time. The known range of this bat in Arkansas now extends over most of the western one-fourth of the State. Until recently this bat has been referred to the species *C. rafinesquii* but Handley (1955) has called attention to the applicability of this name to the eastern species formerly called *C. macrotis* and the priority of the name *C. townsendii* Cooper for the western species.

Specimens examined.—UADZ, CNHM, USNM, total 19. CRAWFORD CO.: Bluff Dweller's Cave-Rudy (1); MADISON CO.: Mitchell Cave-Alabam (1); WASHINGTON CO.: Hewlitt Cave-Fayetteville (2), Basset Cave-Hicks (1), Devil's Icebox Cave-Winslow (11), (2-CNHM), (1-USNM).

Additional specimens.—total 2. CRAWFORD CO.: Mulberry (1-KU); SEVIER CO.: East of Ultamathule, Oklahoma (1-ODZ).

Other records.—WASHINGTON CO.: Devil's Den Cave (1 observed)—Sealander and Young (1955).

CORYNORHINUS RAFINESQUII (Lesson)—Eastern Lump-nosed Bat

Only one record of this bat is known for the State. The specimen (alcoholic), an immature female, was taken on the Osage River, Carroll County—? (Black, 1936) and was originally reported by G. M. Allen (1916). On presumptive grounds this species should occur over most of the eastern two-thirds of Arkansas.

Specimens examined.—MCZ, total 1. CARROLL CO.: Osage River (1-MCZ).

Family DASYPODIDAE

DASYPUS NOVEMCINCTUS MEXICANUS Peters—Nine-banded Armadillo

Armadillos are fairly common in some of the southern counties in the State that border on Louisiana. They are well established in southwestern Arkansas (Black, 1944) and are gradually extending their range in a general northeasterly direction. At present this species has been recorded from thirty-three counties south and west of a line connecting Madison, Van Buren, Jefferson, Lincoln and Chicot counties. The most northerly and northeasterly records thus far are from five miles southeast of Bee Branch, Van Buren County, where one was observed in 1952, and from one mile south of Hindsville, Madison County, where one was found on the Witt farm on June 6, 1954. According to Fitch, Goodrum, and Newman (1952), Buchanan and Talmage (1954), and Talmage and Buchanan (1954) the range of the armadillo extends approximately 100 miles north of the Louisiana line in Arkansas. Records obtained by the writer indicate a considerably more extensive range for this mammal in the State, particularly in the northwestern portion.

Apparently the armadillo is at the present time actively extending its range in Arkansas to the north and east. This range expansion may be favored by changes in agricultural practices as well as by a series of mild winters. The armadillo is notably intolerant of cold and may be exterminated completely or undergo severe reduction in numbers in the northern part of its range by protracted winter cold (Talmage and Buchanan, 1954). Thus, it may periodically extend its range northward under favorable climatic conditions and have its range contracted again by a particularly severe cold wave or by a series of cold winters. Evidence for this hypothesis is accumulating.

In 1921 and in the late thirties this mammal was present in northwestern Arkansas as far north as Cane Hill and Durham in Washington County (Dellinger and Black, 1940). After 1938 it seemed to disappear north of the Arkansas River and no more reports were obtained until 1952 when it was reported from Pope and Van Buren counties. In 1953 and 1954 it reappeared again at Winslow and West Fork in Washington County and was first reported from Madison County. Whether this species will continue to expand its range much further in the State is problematical and may depend largely upon climatic conditions. Certainly, there is little physiological basis for believing that the armadillo will gradually become acclimated to a colder climate and permanently maintain occupancy of its present range in northern Arkansas.

Specimens examined.—UADZ, total 1. WASHINGTON Co.: Durham (1).

Other records.—ASHLEY Co.: Fountain City, 1947, Hamburg, 1947—Fitch, Goodrum and Newman (1952), Reported, 1955—W. A. Kelley; BRADLEY Co.: Reported, 1955—F. Belin and E. Williams; CALHOUN Co.: Reported, 1954, 1955—L. G. Ivy, 1955—R. Hannegan; CHICOT Co.: Reported, 1955—H. B. Routt; CLARK Co.: Hollywood, 1941—Fitch, Goodrum and Newman (1952), Okolona, 1951—J. Robertson. CLEVELAND Co.: New Edinburg, 1947—Fitch, Goodrum, and Newman (1952); COLUMBIA Co.: Reported, 1953—W. D. Lewis, 1955—J. R. Le Fevers; CRAWFORD Co.: Van Buren—Black (1944); DREW Co.: 1948—Fitch, Goodrum and Newman (1952); FRANKLIN Co.: Altus—Dellinger and Black (1940); GARLAND Co.: Reported, 1955—J. A. McQuerry; HEMPSTEAD Co.: Reported—Dellinger and Black (1940), Arkadelphia, 1948—Fitch, Goodrum and Newman (1952), reported, 1955—E. J. Barham; HOT SPRING Co.: Bismark, 1946—Fitch, Goodrum and Newman (1952), reported, 1955—E. Spears and O. L. Gardin; HOWARD Co.: Reported, 1955—W. Kesterson; JEFFERSON Co.: Redfield and Herndale, 1952—B. Ragan, reported, 1955—B. Lawrence and B. Ragan; LAFAYETTE Co.: Lewisville, 1947—Fitch, Goodrum and Newman (1952); LINCOLN Co.: Reported, 1955—R. D. Norris; LITTLE RIVER Co.: Texarkana—Dellinger and Black (1940); LOGAN Co.: Paris—Dellinger and Black (1940); MADISON Co.: Hindsville, 1954—R. J. Parker; MILLER Co.: Doddridge, 1930, 1946, 1948, Fouke, 1930—Fitch, Goodrum and Newman (1952), Texarkana—Dellinger and Black (1940), reported, 1954—M. D. Cummings; NEVADA Co.: Reported 1955—B. B. Haynie; OUACHITA Co.: Chidester, 1955—W. E. Shankle, reported, 1955—J. M. Dawson; PERRY Co.: Perryville, 1952—E. D. Hill; PIKE Co.: Daisy, 1947 Fitch, Goodrum and Newman (1952), reported, 1954—M. D. Cummings; POLK Co.: Reported, 1955—I. A. Hilton; POPE Co.: Dover, 1952—O. Freeman; SCOTT Co.: Hon, 1946—K. Taff; SEBASTIAN Co.: Barling—Dellinger and Black (1940); SEVIER Co.: Horatio, 1945, 1946, 1949—Fitch, Goodrum and Newman (1952); UNION Co.: Strong, 1948, Eldorado, 1948—Fitch, Goodrum and Newman (1952), reported, 1951—A. J. Hoiberg, reported, 1953—W. D. Lewis, Eldorado, 1953—A. J. Hoiberg; VAN BUREN Co.: Bee Branch, 1952—Hulen McKim; WASHINGTON Co.: Cane Hill and Durham—Dellinger and Black (1940), Winslow, 1953—H. F. Kratz, West Fork, 1953—M. A. Jacobs.

Family LEPORIDAE

LEPUS CALIFORNICUS MELANOTIS Mearns

Black (1936) first reported the jackrabbit from Benton, Crawford, and Washington counties. A few years later there was some evidence that jackrabbits had increased in numbers in these counties (Dellinger and Black, 1940). This species seems to have expanded its range still farther in the last few years. Before 1935 there were few reports of jackrabbits in the State. They were first observed in Franklin county in 1927 and it is thought that they may have been brought in from Oklahoma by floodwaters of the Arkansas River. A few are still present in southern Franklin County. Apparently this

species has been expanding its range in Arkansas as clearing of the land has opened up suitable habitat. At present it is locally common in Benton, Crawford, and Washington counties. No further range extension is foreseen in the heavily forested areas of northern Arkansas, but any sudden increase in numbers in the southern portion of its range in the State might be accompanied by further invasion of the Arkansas River Valley.

Specimens examined.—UADZ, total 3. WASHINGTON Co.: Fayetteville-(2), Tontitown-(1).

Other records.—BENTON Co.: Maysville—Black (1936), Gravette—Dellinger and Black (1940), reported, 1955—J. Bagget; CARROLL Co.: Berryville—survey of Arkansas Game (1951); CRAWFORD Co.: Mountainburg—Black (1936), 2 miles S Evansville—Dellinger and Black (1940), reported, 1955—L. McBride; FRANKLIN Co.: Reported, 1927, 1955—W. Walls; GARLAND Co.: Lonsdale, 1955—G. Hatzakas; LOGAN Co.: Magazine, 1955—K. Taff; MADISON Co.: Reported, 1955—V. Weathers; WASHINGTON Co.: Evansville, Lincoln, Prairie Grove, Springdale, Summers, Winslow—Black (1936), Farmington, Fayetteville, Prairie Grove, Tontitown—Dellinger and Black (1940), Fayetteville, 1955—E. Whattley, reported, 1955—P. Baxter, R. J. Parker and J. Abshier; YELL Co.: Belleville, 1954—R. J. Parker.

SYLVILAGUS FLORIDANUS ALACER (Bangs)—Oklahoma Cottontail

Cottontails are numerous throughout the State and occur in a wide variety of habitats. They are most common in briar patches and brushy areas in both rural and urban areas. Together with the opossum and common skunk they are subject to a high mortality rate on the highways.

Specimens examined.—UADZ, total 11. BENTON Co.: 4 miles NE Springdale-(1); GARLAND Co.: Avant (1); RANDOLPH Co.: Dalton (1); WASHINGTON Co.: Fayetteville (4), Lake Wedington Area (1), Prairie Grove (2), West Fork (1).

Additional specimens.—total 22. ARKANSAS Co.: Stuttgart (1-BS); BOONE Co.: Bergman (5-MVZ); CRAWFORD Co.: Mountainburg (1-KU); GREENE Co.: Paragould (1-MNS); MADISON Co.: Pettigrew (1-BS); MONTGOMERY Co.: Mt. Ida, (1-MNS); PIKE Co.: Delight (3-BS), (1-MZM); STONE Co.: Marcella (4-CNHM); WASHINGTON Co.: Fayetteville (2-MZM), Winslow (2-KU).

Other records.—CONWAY Co.: Morrilton—W. Britt (*pers. comm.*); JEFFERSON Co.: Pine Bluff—J. A. Sealander; LAWRENCE Co.: Walnut Ridge—J. A. Sealander; LONOKE Co.: Lonoke—A. H. Hulsey (*in. litt.*); NEWTON Co.: Jasper (in bobcat stomach examined by writer); PERRY Co.: Bigelow—H. Newman (*pers. comm.*); POPE Co.: Russellville (in coyote stomach examined by writer); PULASKI Co.: Mayflower—C. W. Nelson (*pers. comm.*), Maumelle (in bobcat stomach examined by writer), Roland (in bobcat stomach examined by writer); SEBASTIAN Co.: Fort Smith—Lyndal York (*in. litt.*); reported from all remaining counties in State by game wardens and other personnel of the Arkansas Game and Fish Commission.

SYLVILAGUS AQUATICUS AQUATICUS (Bachman)—Swamp Rabbit

Swamp rabbits are locally common throughout Arkansas. They occur principally in bottomland swampy areas and in canebrakes and brushy areas along streams. This species is very common in eastern and south-central parts of the State but is less numerous in western Arkansas and in the Ozark and Ouachita mountain regions. In the Ozarks swamp rabbits are locally abundant along the Illinois, White, and Black rivers.

Specimens examined.—UADZ, total 2. WASHINGTON Co.: Fayetteville (2).

Additional specimens.—total 7. PIKE Co.: Delight, (1-BS); STONE Co.: Marcella (4-CNHM); WASHINGTON Co.: Fayetteville (2-MZM).

Other records.—ARKANSAS CO.: Stuttgart (1)—Dellinger and Black (1940); JEFFERSON CO.: Pine Bluff—numerous observations by D. A. James, R. G. Leonard, J. P. Redman and J. A. Sealander; LOGAN CO.: New Blaine (in coyote stomach examined by writer); LONOKE CO.: Lonoke—A. H. Hulsey (*pers. comm.*); PULASKI CO.: Mayflower—C. W. Nelson (*pers. comm.*); WASHINGTON CO.: Elkins, Prairie Grove, Springdale—Black (1936); WOODRUFF CO.: Augusta (2)—Dellinger and Black (1940); reports have also been received from game wardens and other officials of the Arkansas Game and Fish Commission in the following counties: Ashley; Benton; Bradley; Calhoun; Chicot; Clark; Clay-Black River bottoms; Cleburne; Cleveland; Columbia; Crawford; Crittenden; Cross-L'anguille bottoms; Dallas; Franklin; Fulton-Spring River, English Creek, Wyatt Creek; Garland-Ouachita River bottoms; Hempstead; Hot Spring; Independence; Jackson; Lawrence; Lee; Lincoln; Miller; Mississippi; Monroe-White River bottoms; Nevada; Ouachita; Perry; Phillips; Poinsett; Prairie; Randolph; Scott; Searcy-Red River bottoms; Sevier; Sharp-Straw River, Spring River; St. Francis-St. Francis River, Caneville River bottoms; Union, Yell.

Family SCIURIDAE

MARMOTA MONAX MONAX (Linnaeus)—Southern Woodchuck

Woodchucks are common in the wooded, hilly areas of northern and western Arkansas. They are scarce or rare east of a line connecting Clay, Monroe, and Lincoln counties and seem to be absent in nearly all counties along the Mississippi River. This species is uncommon or scarce in most counties south of the Arkansas River and apparently is absent in most of the southern one-third of the State. It has not been reported from any of the counties adjacent to Louisiana. The most southerly record of its occurrence is from Hempstead County in western Arkansas. A Louisiana record from Shreveport (G. H. Lowery, *in. litt.*) suggests that the range of this species may extend from Hempstead County across the border into Louisiana. Albino woodchucks occur occasionally. One was reported by Dellinger and Black (1940) and a family of albino woodchucks is located about five miles southwest of Hindsville, Madison County.

Specimens examined.—UADZ, total 6. MADISON CO.: Huntsville (1); WASHINGTON CO.: Fayetteville (3), Goshen (1), Lake Wedington Area (1).

Additional specimens.—total 11. BOONE CO.: Bergman (1-MVZ); STONE CO.: Marcella (1-CNHM). WASHINGTON CO.: Fayetteville (1-CNHM), (2-KU), West Fork (2-KU), Winslow (4-KU).

Other records.—FRANKLIN CO.: Cass (1)—Cass (1)—Dellinger and Black (1940); MADISON CO.: Hindsville, R. J. Parker (*in litt.*); MARION CO.: Yelleville—Dellinger and Black (1940); NEWTON CO.: Marble Falls (1)—Dellinger and Black (1940); PERRY CO.: Ledwidge, E. D. Hill (*in. litt.*); reports have been received from game wardens and other officials of the Arkansas Game and Fish Commission in the following counties: Baxter; Benton; Carroll; Clay; Cleburne; Crawford; Cross; Fulton; Garland; Hempstead; Hot Springs; Independence; Jackson; Lee; Lincoln; Lonoke; Monroe; Montgomery; Pike; Poinsett; Prairie; Randolph; Searcy; Sharp; Yell.

TAMIAS STRIATUS VENUSTUS Bangs—Southwestern Chipmunk

Chipmunks are common throughout the wooded areas of the Ozarks and in the Ouachita mountains south of the Arkansas River. They seem to be absent south of a line connecting Hempstead, Dallas, Lonoke, and Phillips counties and apparently are rare or absent in most of the eastern one-fourth of the State.

Specimens examined.—UADZ, total 11. CRAWFORD CO.: Natural Dam (1); GARLAND CO.: Avant (2); POPE CO.: Pelsor (1); WASHINGTON CO.: Fayetteville (3), Goshen (2), Johnson (1), Rhea (1).

Additional specimens.—total 51. BOONE CO.: Bergman (9-MVZ), Olvey 6-MVZ), Zinc (1-MVZ); CRAWFORD CO.: Van Buren (2-BS); MADISON CO.: Pettigrew (1-BS); PIKE CO.: Delight (12-BS), (3-MCZ); POLK CO.: Rich Mountain (1-BS); WASHINGTON CO.: Fayetteville (12-KU), Winslow (4-KU).

Other records.—BENTON CO.: Gravette—Black (1936); CARROLL CO.: Bush (1)—D. M. Moore (*pers. comm.*); CRAWFORD CO.: Mountainburg—Black (1936), Beaver Dam—Dellinger and Black (1940); FRANKLIN CO.: Cass (1)—Dellinger and Black (1940), Ozark—Black (1936). Reports have been received from Arkansas Game and Fish Commission personnel in the following counties: Baxter; Clay; Cleburne; Dallas; Fulton; Hempstead; Hot Spring; Howard; Independence; Jackson; Lonoke; Marion; Perry; Phillips; Prairie; Randolph; Scott; Searcy; Sharp; Stone; Yell.

SCIURUS CAROLINENSIS CAROLINENSIS Gmelin—Southern Gray Squirrel

The gray squirrel is state wide in distribution. It is commoner in the heavily wooded areas of the State, particularly in the bottomland hardwood forests of eastern Arkansas. Melanistic and albinistic individuals are not uncommon. The black color phase occurs frequently although it is not as common as in the fox squirrel. White or partially white individuals are occasional in occurrence. A colony of white or albinistic gray squirrels has been located in the vicinity of Jonesboro, Craighead County, for several years. The writer has not had the opportunity to observe this colony and has not been able to ascertain the approximate percentage of pure albinism found in the colony.

Mass outbreaks of both gray and fox squirrels have occurred at irregular intervals in the past. In 1936 mass migrations occurred in Howard, Perry, Pike, Polk, and Sevier counties, and an outbreak among gray squirrels occurred in the Ouachita River bottoms in 1942 (cf. A survey of Arkansas game, 1951).

Specimens examined.—UADZ, total 11. GRANT CO.: Sheridan (1); POINSETT CO.: Wiener (2); RANDOLPH CO.: Dalton (1); UNION CO.: 11 miles N. Strong (1); WASHINGTON CO.: 15 miles W. Fayetteville (1), Johnson (1), Rhea (1), Springdale (1).

Additional specimens.—total 29. BOONE CO.: Bergman (8-MVZ); CLAY CO.: Greenway (5-CNHM); MONTGOMERY CO.: Mt. Ida (1-MNS); PIKE CO.: Delight (2-BS); POLK CO.: Rich Mountain (1-BS); STONE CO.: Marcella (1-CNHM); WASHINGTON CO.: Winslow (10-KU), 1-MZM).

Other records.—INDEPENDENCE CO.: Batesville—W. L. Henning (*in. litt.*); JEFFERSON CO.: Pine Bluff—J. P. Redman (*pers. comm.*); LONOKE CO.: Two Prairie Bayou—A. H. Hulsey (*in litt.*); PERRY CO.: Bigelow (1)—H. Newman (*pers. comm.*); SEBASTIAN CO.: Monte Vista—Lyndal York (*in. litt.*); reported from remaining counties in State by personnel of the Arkansas Game and Fish Commission.

SCIURUS NIGER RUFIVENTER E. Geoffroy-Saint-Hilaire—Mississippi Valley Fox Squirrel

Fox squirrels are abundant in all parts of the State. Melanistic individuals are very common, particularly in bottomland areas. It has been stated that over 50 per cent of the fox squirrel population in the bottomlands of Arkansas, Desha and Chicot counties are melanistic (cf. A survey of Arkansas game, 1951). Intergradation with the race *subauratus* may occur in southeastern Arkansas, and intermediates between *rufiventer* and the race *ludovicianus*

probably occur in southwestern Arkansas (G. H. Lowery, *in litt.*; Lowery, G. H. and W. B. Davis, 1942). Too few specimens are available at present to determine whether the races *subauratus* and *ludovicianus* extend into Arkansas.

Specimens examined.—UADZ, total 13. JEFFERSON Co.: Pine Bluff (1); MONTGOMERY Co.: Mt. Ida (2); PERRY Co.: Bigelow (1); UNION Co.: El Dorado (1); WASHINGTON Co.: Fayetteville (3), Goshen (2), Johnson (1), Lake Wedington Area (1); WOODRUFF Co.: Augusta (1); YELL Co.: Danville (1).

Additional specimens.—total more than 25. BOONE Co.: Bergman (11-MVZ), Zinc (1-MVZ); CRAWFORD Co.: Van Buren (1-BS); DESHA Co.: Big Island (several-ASM); MONTGOMERY Co.: Mt. Ida (1-MNS); STONE Co.: Marcella (2-CNHM); WASHINGTON Co.: Fayetteville (1-MZM); Winslow (8-KU).

Other records.—CONWAY Co.: Morrilton (1)—W. Britt (*pers. comm.*); LONOKE Co.: Bayou Meto—A. H. Hulsey (*in. litt.*); PERRY Co.: Bigelow (5)—H. Newman (*pers. comm.*); SEBASTIAN Co.: Monte Vista—Lyndal York (*in. litt.*); reported from remaining counties in State by personnel of the Arkansas Game and Fish Commission.

GLAUCOMYS VOLANS VOLANS (Linnaeus)—Small Eastern Flying Squirrel
GLAUCOMYS VOLANS SATURATUS A. H. Howell—Southeastern Flying Squirrel

The flying squirrel is common in wooded areas throughout the State. The race *volans* occupies the northernmost tier of counties where it intergrades with and is replaced by the race *saturatus* to the south. Black (1936) tentatively established the demarcation line between the two races at 1600 feet and below on the southern boundaries of Washington and Madison counties. Specimens from Washington County have been referred to the race *volans* chiefly on the basis of measurements as pelage characteristics are more typical of the race *saturatus*. It seems probable that most of the specimens from northern Arkansas that are referable to the nominate race may be intergrades.

Specimens examined.—UADZ, total 8. BRADLEY Co.: 11 miles N Strong (1); GARLAND Co.: Avant (1); JEFFERSON Co.: Pine Bluff (2); POLK Co.: 6 miles W Rich Mountain (1); WASHINGTON Co.: Fayetteville (3).

Additional specimens.—total 18. BOONE Co.: Bergman (5-MVZ); DREW Co.: Monticello (2-MNS); MONTGOMERY Co.: 8 miles N Mt. Ida (1-MNS); PIKE Co.: Delight (2-BS); WASHINGTON Co.: Winslow (8-KU).

Other records.—MONROE Co.: 6 miles NE Holly Grove—T. E. Oliphant; SEBASTIAN Co.: Fort Smith—Lyndal York (*in. litt.*); reports have been received from personnel of the Arkansas Game and Fish Commission in the following counties: Ashley; Baxter; Benton; Calhoun; Carroll; Clark; Clay; Cleburne; Cleveland; Columbia Crawford; Crittenden; Cross; Dallas; Franklin; Fulton; Hempstead; Hot Spring; Howard; Independence; Izard; Jackson; Lawrence; Lee; Lincoln; Lonoke; Madison; Marion; Nevada; Ouachita; Perry; Phillips; Poinsett; Prairie; Randolph; Scott; Searcy; Sharp; Union; Woodruff; Yell.

Family GEOMYIDAE

GEOMYS BURSARIUS DUTCHERI Davis—Oklahoma Pocket Gopher

The pocket gopher ranges throughout the Arkansas River Valley on both sides of the Arkansas River. It seems to be much more common south of the Arkansas River and is quite common throughout the south-central portion of the State and in the border counties adjacent to Louisiana. It occurs sparingly along the Mississippi Valley as far north as Cross County.

Specimens examined.—UADZ, total 23. COLUMBIA CO.: Magnolia (18); JEFFERSON CO.: Pine Bluff (1); OUACHITA CO.: Cullendale (1); SEBASTIAN CO.: Fort Smith (1); UNION CO.: El Dorado (2).

Additional specimens.—total 24. OUACHITA CO.: Camden (1-USNM); SALINE CO.: Benton (7-USNM); SEBASTIAN CO.: Fort Smith (7-USNM), (7-LY), (2-MNS).

Other records.—CRAWFORD CO.: Mulberry—Black (1936); FRANKLIN CO.: Ozark—Black (1936); PULASKI CO.: 10 miles N Little Rock—C. W. Nelson (*pers. comm.*); SEBASTIAN CO.: Mansfield (1)—Dellinger and Black (1940); reports have been received from personnel of the Arkansas Game and Fish Commission in the following counties: Ashley; Bradley; Chicot; Cross; Dallas; Garland; Hempstead; Hot Spring; Madison; Nevada; Phillips; Washington.

Family CASTORIDAE

CASTOR CANADENSIS CAROLINENSIS Rhoads—Southern Beaver

CASTOR CANADENSIS MISSOURIENSIS V. Bailey—Missouri River Beaver

At one time the beaver was common throughout the State but was exterminated soon after 1900. Presumably the race *carolinensis* originally occupied most of Arkansas, although the race *texensis* probably occurred in the Red River basin in southwestern Arkansas. Over 50 individuals of the race *carolinensis* were released in the State between 1943 and 1945 by the Arkansas Game and Fish Commission. All of the releases were at least partially successful and the beaver population appears to be increasing throughout the State. A few beaver, presumably of the race *missouriensis*, entered from Missouri into Baxter County, Arkansas in 1942 and then moved into Stone County. Since this original invasion beaver colonies have been established in Washington and Clay counties where no stocking has been undertaken by the Arkansas Game and Fish Commission. Presumably beaver in these counties entered from Missouri or the Washington County beavers may have come from Oklahoma. A few beavers are now present in most of the northern tier of counties. Some of these may have moved northward from thriving colonies in more southern counties, while a few may have been introduced by personnel of the game and fish commission. Six beavers of the race *canadensis* were introduced into Ashley County in 1934. Beavers are still present in Ashley County, although they were reported scarce in 1955. Whether these beaver are progeny of this original introduction or have resulted from later plantings is not known.

Specimens examined.—None.

Other records.—Beavers have been reported either as the result of invasions from neighboring states or introductions by the Arkansas Game and Fish Commission, from the following counties by personnel of the Arkansas Game and Fish Commission: Ashley; Baxter; Benton; Boone; Bradley; Calhoun; Carroll; Clark; Clay; Cleburne; Conway; Crawford; Crittenden; Cross; Dallas; Garland; Hempstead; Hot Spring; Howard; Independence; Lee; Lincoln; Madison; Marion; Montgomery; Nevada; Ouachita; Phillips; Pike; Polk; Pulaski; Randolph; Saline; Searcy; Sevier; St. Francis; Stone; Washington; Yell.

Family CRICETIDAE

ORYZOMYS PALUSTRIS TEXENSIS J. A. Allen—Texas Rice Rat

Rice rats are nearly state wide in distribution. Possibly they may be absent in a small portion of southwestern Arkansas and in some of the northern

counties adjacent to Missouri. However, systematic trapping is likely to reveal their presence in these areas as well. In the northwestern part of the State this species seems to be common in isolated localities but is not generally distributed (Davis and Lidicker, 1955). In central and eastern portions of the State rice rats are quite common, particularly along irrigation ditches and in rice fields. Expansion of the rice industry in the State in recent years has undoubtedly increased the total population of this rodent in the State by creating more suitable habitat.

Specimens examined.—UADZ, total 6: JEFFERSON CO.: Pine Bluff (1); PULASKI CO.: Little Rock (4); WASHINGTON CO.: Johnson (1).

Additional specimens.—Total 13. ASHLEY CO.: Wilmot (1-BS); BENTON CO.: 8 miles E Siloam Springs (5-IU); CRAIGHEAD CO.: Lake City (1-BS); MILLER CO.: Fulton (1-CNHM); OUACHITA CO.: Camden (2-BS); PIKE CO.: Delight (1-BS); POLK CO.: Rocky (1-KU); PULASKI CO.: Little Rock (1-MVZ).

Other records.—ARKANSAS CO.: Stuttgart (1)—Dellinger and Black (1940); POPE CO.: Russellville (3)—E. B. Holmes (*in. litt.*).

REITHRODONTOMYS HUMULIS (Audubon and Bachman)—Eastern Harvest Mouse

A single specimen has been collected in the State. The specific identity has been confirmed by Dr. Emmet T. Hooper, Museum of Zoology, University of Michigan, but no subspecific assignment has been made.

Specimens examined.—MNS, total 1. SEBASTIAN CO.: Fort Smith (1).

REITHRODONTOMYS MEGALOTIS DYCHEI J. A. Allen—Prairie Harvest Mouse

Three specimens were collected in Mississippi County in 1951 (Sealander, 1954). Presumably they occur throughout the extreme northeastern corner of the State.

Specimens examined.—UADZ, total 3. MISSISSIPPI CO.: Leachville (3).

REITHRODONTOMYS FULVESCENS AURANTIUS J. A. Allen—Golden Harvest Mouse

Undoubtedly this species is state wide in distribution although it has not been recorded from the eastern one-fourth of the State. It is one of the most common small mammals in Arkansas and occurs in open, grassy or shrubby areas and along fence rows. Harvest mice are often found in old fields that have become covered with broom sedge and their nests are frequently found in dense stands of broom sedge.

Specimens examined.—UADZ, total 26. GARLAND CO.: Avant (5); HEMPSTEAD CO.: McNab (1); JEFFERSON CO.: Pine Bluff (6); PERRY CO.: Bigelow (1); POLK CO.: Mena (2); SEBASTIAN CO.: Barling (2); UNION CO.: El Dorado (2); WASHINGTON CO.: Fayetteville (4); Lake Wedington Area (3).

Additional specimens.—total 36 plus. BENTON CO.: 8 miles E Siloam Springs (IU); BOONE CO.: Valley Springs (9-KU); CRAWFORD CO.: Mountainburg (1-MNS); MADISON CO.: Huntsville (1-KU); PIKE CO.: Delight 4-BS), (1-CNHM), (1-MZM); POLK CO.: Mena (4-KU), Rocky (2-KU); SEBASTIAN CO.: Fort Smith (2-LY); STONE CO.: Marcella (3-CNHM); UNION CO.: Calion (2-AJH); WASHINGTON CO.: 8 miles W Springdale (IU), Winslow (4-KU); WHITE CO.: Beebe (2-BS).

Other records.—FRANKLIN CO.: Cass (1)—Dellinger and Black (1940); MILLER

Co.: Texarkana (2)—R. B. Loomis (*in. litt.*); POPE Co.: Caglesville (1), Dardanelle (2), Russellville (5), Scottsville (2)—E. B. Holmes, (*in. litt.*).

PEROMYSCUS MANICULATUS BAIRDII (Hoy and Kennicott)—
Prairie Deer Mouse

PEROMYSCUS MANICULATUS OZARKIARUM Black—Ozark White-footed Mouse

This species is probably state wide in distribution although no specimens have been collected from the southern one-fourth of the State. Most of the specimens collected in the State are referable to the race *ozarkiarum*. A few individuals collected by Black near Barling, Sebastian County, have been referred to the race *bairdii* by Dr. D. H. Johnson, U. S. National Museum, Washington, D.C. According to Black (*in. litt.*) the Barling mice were collected on the banks of the Arkansas River and may represent upstream refugees from Oklahoma.

Specimens examined.—UADZ, total 18. GARLAND Co.: Buckville (1); JEFFERSON Co.: Pine Bluff (2); LOGAN Co.: Mt. Magazine (3); MISSISSIPPI Co.: Leachville (1); POLK Co.: Mena 2); SEBASTIAN Co.: Barling (1); WASHINGTON Co.: Fayetteville (6), Winslow (2).

Additional specimens.—total 66 plus. BENTON Co.: Gravette (2-KU), 8 miles E Siloam Springs (IU); FRANKLIN Co.: Fly Gap Tower (2-CNHM); MADISON Co.: Huntsville (2-KU); STONE Co.: Marcella (3-CNHM); WASHINGTON Co.: Winslow (49-KU), (8-MVZ).

Other records—POPE Co.: Mill Creek (2), Russellville (7)—E. B. Holmes (*in. litt.*); ST. FRANCIS Co.: Forrest City (2)—R. B. Loomis (*in litt.*).

PEROMYSCUS LEUCOPUS LEUCOPUS (Rafinesque)—
Southern White-footed Mouse

PEROMYSCUS LEUCOPUS NOVEBORACENSIS (Fischer)—
Northern White-footed Mouse

This is a very common species and occurs abundantly in woodland and shrubby habitat throughout the State. There is a large amount of intergradation between the northern race, *noveboracensis*, and the southern race, *leucopus*. A majority of the specimens collected in Arkansas are referable to the nominate race. Specimens from Boone, Crawford, Franklin, Fulton, Madison, Sharp, and Washington counties have been referred to the race *noveboracensis*. Most of these specimens are intermediate between *leucopus* and *noveboracensis* and the zone of intergradation extends as far south as Sebastian and Logan counties. Further study will be necessary before most of the specimens from northern Arkansas can be given any definite subspecies assignment. The evidence seems to point to a very gradual cline in characters shared by the two races which may extend as far north as central Illinois.

Specimens examined.—UADZ, USNM, total 35. BENTON Co.: Rogers (1); CRAWFORD Co.: Natural Dam (1); JEFFERSON Co.: Pine Bluff (7); POLK Co.: Eagleton (1), Rich Mountain (2); SEBASTIAN Co.: Barling (3), (1-USNM), Fort Smith (1); UNION Co.: El Dorado (2); WASHINGTON Co.: Fayetteville (9), Goshen (1), Johnson (4), Lake Wedington Area (1), Mt. Comfort (1).

Additional specimens.—total 57 plus. ARKANSAS Co.: Stuttgart (1-BS); BENTON Co.: 8 miles E Siloam Springs (IU); BOONE Co.: Valley Springs (2-KU); CRAW-

FORD Co.: Mountainburg (1-KU); CRITTENDEN Co.: Big Creek (1-BS); FULTON Co.: Mammoth Springs (1-KU); MADISON Co.: Huntsville (2-KU), Pettigrew (1-BS); PIKE Co.: Delight (8-BS); POLK Co.: Hatfield (1-KU), Rocky (1-KU); SHARP Co.: Hardy (4-BS); STONE Co.: Marcella (1-KU); WASHINGTON Co.: Fayetteville (3-KU), (1-BS), Winslow (26-KU), (2-MVZ), Wyman (1-MVZ).

Other records.—FRANKLIN Co.: Cass (1)—Dellinger and Black (1940); POLK Co.: Wickes (2)—R. B. Loomis (*in. litt.*); ST. FRANCIS Co.: Forrest City (2)—R. B. Loomis (*in litt.*).

PEROMYSCUS GOSSYPINUS MEGACEPHALUS (Rhoads)—Rhoads Cotton Mouse

The cotton mouse occurs in most of the southern two-thirds of the State. It is found in the same type of habitat as *Peromyscus leucopus* and there is a definite overlap in their ecological distribution. However, this species seems to inhabit low woods and swampy areas more often than *P. leucopus*.

Specimens examined.—UADZ, USNM, total 38. GARLAND Co.: Avant (5), Buckville (1), Cedar Glades (3), (2-USNM); JEFFERSON Co.: Pine Bluff (3); POLK Co.: Eagleton (3), Mena (4), 11 miles SE Mena (2); PULASKI Co.: Little Rock (13); UNION Co.: Eldorado (2).

Additional specimens.—total 8. CRITTENDEN Co.: Big Creek (7-USNM); MILLER Co.: Texarkana (1-BS).

Other records.—POLK Co.: Mena (1)—R. B. Loomis (*in. litt.*); POPE Co.: Russellville (5)—Dellinger and Black (1940); SEBASTIAN Co.: Barling (6)—Dellinger and Black (1940).

PEROMYSCUS BOYLII ATTWATERI J. A. Allen—Attwater Brush Mouse

The brush mouse is found in northern and western portions of the State in association with limestone and sandstone outcroppings. It is often seen in caves.

Specimens examined.—UADZ, total 11. CRAWFORD Co.: Natural Dam (6); GARLAND Co.: Avant (2), Cedar Glades (1); POLK Co.: Eagleton (1), Mena (1).

Additional specimens.—total 32. BOONE Co.: Lowry (1-KU); FRANKLIN Co.: Fly Gap Tower (6-CNHM), Ozark (5-KU); INDEPENDENCE Co.: Batesville (3-BS); LOGAN Co.: Mt. Magazine (3-CNHM); MADISON Co.: Pettigrew (1-BS); POLK Co.: Rich Mountain (2-BS); STONE Co.: Marcella (14-CNHM), (2-KU); WASHINGTON Co.: Winslow (7-KU).

PEROMYSCUS NUTTALLI FLAMMEUS Goldman—Southern Golden Mouse

Golden mice occur throughout the State but only a few specimens have been taken in the northern half. No specimens have been taken in northeastern Arkansas, although the species undoubtedly occurs there. This mammal is locally abundant in the southern half of the State and seems to be most common in the oak-pine uplands of eastern Arkansas.

Specimens examined.—UADZ, total 10. CHICOT Co.: Island No. 80 (1); GARLAND Co.: Buckville (1); JEFFERSON Co.: Pine Bluff (2); POLK Co.: Mena (1), 6 miles W Rich Mountain (2), Shady Lake Area (1); UNION Co.: El Dorado (1); WASHINGTON Co.: Fayetteville (1).

Additional specimens.—total 27. CRITTENDEN Co.: Big Creek (1-BS); PIKE Co.: Delight (4-MCZ); SCOTT Co.: Fourche La Fave River, (2-CNHM); WASHINGTON Co.: Winslow (19-KU); WHITE Co.: Beebe (1-BS).

SIGMODON HISPIDUS HISPIDUS Say and Ord—Northern Cotton Rat
SIGMODON HISPIDUS TEXIANUS (Audubon and Bachman)—Texas Cotton Rat

Cotton rats are very common throughout the State and in some agricultural areas are numerous enough to be important crop pests (Sealander and Walker, 1955). The nominate race occupies all of Arkansas except the western edge of the State in which the race *texianus* and intermediates between the races *texianus* and *hispidus* are found.

Specimens examined.—UADZ, IU, total 55. BENTON Co.: 1 mile N Springdale (5), (1-IU); GARLAND Co.: Avant (3); JEFFERSON Co.: Pine Bluff (1); MISSISSIPPI Co.: Leachville (2); PERRY Co.: Bigelow (1); POLK Co.: Mena (1); POPE Co.: Russellville (7); PULASKI Co.: Little Rock (2); SEBASTIAN Co.: Fort Smith (2); UNION Co.: El Dorado (1); WASHINGTON Co.: Fayetteville (19), (5-IU), Johnson (4), Lake Wedington Area (1).

Additional specimens.—total 98. BENTON Co.: 8 miles E Siloam Springs (IU); BOONE Co.: Harrison (3-KU), Valley Springs (40-KU); MADISON Co.: 20 miles W Huntsville (1-MVZ); MILLER Co.: Fulton (1-CNHM); MONROE Co.: Monroe (1-MNS); PIKE Co.: Delight (8-BS), (1-MZM); POLK Co.: Rocky (2-KU); SEBASTIAN Co.: Fort Smith (2-LY), (1-MNS); STONE Co.: Marcella (6-CNHM); WASHINGTON Co.: Winslow (32-KU).

Other records.—BENTON Co.: Gravette (2)—Black (1936); FRANKLIN Co.: Ozark (1)—Black (1936); LOGAN Co.: New Blain (5)—in coyote stomachs examined by writer; MADISON Co.: Huntsville—Black (1936); POLK Co.: Mena (1)—R. B. Loomis (*in. litt.*); POPE Co.: Mill Creek (1), Russellville (2)—E. B. Holmes (*in. litt.*).

NEOTOMA FLORIDANA ILLINOENSIS A. H. Howell—Illinois Wood Rat
NEOTOMA FLORIDANA OSAGENSIS Blair—Osage Wood Rat

The range of the wood rat includes all of Arkansas. The race *osagensis* is found in the northwestern and western portions of the State and its range extends eastward approximately to a line running from western Fulton County through western Conway, Perry, and Garland counties to eastern Howard, Sevier, and Little River counties. The eastern race *illinoensis* which occupies the remainder of the state intergrades with the race *osagensis*, but the extent of this intergradation is not known. The race *illinoensis*, which has been poorly collected in Arkansas, evidently has a more local distribution than the race *osagensis* which is common in caves and rock outcroppings throughout the Ozarks and the Ouachita Mountains. At present the only records of *illinoensis* are from Crittenden, Desha, and Miller counties. The specimen representing Miller County was actually taken in west Texarkana which is in Bowie County, Texas. It undoubtedly occurs in east Texarkana, Arkansas as well so that Miller County is included within its range in Arkansas.

Specimens examined.—UADZ, total 22. FRANKLIN Co.: White Rock Mountain (1); GARLAND Co.: Avant (2), Cedar Glades (6); POLK Co.: Eagleton (4), Mena (1), 6 miles W Rich Mountain (3); WASHINGTON Co.: Fayetteville (4), Lake Wedington Area (1).

Additional specimens.—total 40. BAXTER Co.: Cotter (3-BS); CRITTENDEN Co.: Big Creek (7-BS); DESHA Co.: McGehee (3-BS); INDEPENDENCE Co.: Batesville (2-BS); LOGAN Co.: Magazine Mountain (1-CNHM); MADISON Co.: Pettigrew

(2-BS); MONTGOMERY Co.: Mt. Ida (1-MNS), Womble (near Norman), (1-BS); PIKE Co.: Delight (2-BS); POLK Co.: Rich Mountain (9-BS); SCOTT Co.: Fourche La Fave River (1-CNHM); STONE Co.: Marcella (8-CNHM).

Other records.—BENTON Co.: War Eagle (1)—Dellinger and Black (1940); FRANKLIN Co.: Ozark—Black (1936); PERRY Co.:—E. D. Hill (*in. litt.*); SEVIER Co.: DeQueen (1)—R. B. Loomis (*in. litt.*); WASHINGTON Co.: Prairie Grove—Black (1936).

SYNAPTOMYS COOPERI GOSSII (Coues)—Goss Lemming Mouse

Only a single record of this species exists for the State. The specimen, which is in the U. S. Biological Survey collection, has been assigned to the race *gossii* (Wetzel, 1955) largely on a distributional basis as it is too young to show the typical racial characteristics. Presumably this species is still found in extreme northeastern Arkansas but is probably very local in occurrence.

Specimens.—BS, total 1. CRAIGHEAD Co.: Lake City (1-BS).

MICROTUS PINETORUM AURICULARIS (V. Bailey)—Bluegrass Pine Vole
MICROTUS PINETORUM NEMORALIS (V. Bailey)—Woodland Pine Vole

The pine vole is locally distributed throughout the State and may be abundant where the habitat is suitable. Because it is apparently more restricted in its habitat requirements than some other small mammals it is not as easily collected. The race *auricularis* occurs in extreme southwestern, southeastern, and eastern portions of the State. A specimen from El Dorado, Union County, in the collection of A. J. Hoiberg has been tentatively assigned to this race. Intergradation probably occurs between this race and the race *nemoralis* which is found in the remainder of the State (cf. Hall and Cockrum, 1953).

Specimens examined.—UADZ, total 9. JEFFERSON Co.: Pine Bluff (1); POLK Co.: Mena (1); PULASKI Co.: Little Rock (2); SEBASTIAN Co.: Barling (1); WASHINGTON Co.: Fayetteville (1), Lake Wedington Area (2), Winslow (1).

Additional specimens.—total 53. ARKANSAS Co.: Stuttgart (1-BS); PIKE Co.: Delight (3-MCZ); POLK Co.: Cove (9-KU), Mena, (7-KU), Rocky (2-KU); SHARP Co.: Hardy (1-BS); STONE Co.: Marcella (2-CNHM); WASHINGTON Co.: Winslow (17-KU), (3-MVZ); WHITE Co.: Beebe (5-BS).

Other records.—CRAWFORD Co.: Beaver Dam (1)—Dellinger and Black (1940); FRANKLIN Co.: Cass (1)—Dellinger and Black (1940); POLK Co.: Mena (1)—R. B. Loomis (*in. litt.*); POPE Co.: Russellville (1)—E. B. Holmes (*in. litt.*).

ONDATRA ZIBETHICUS ZIBETHICUS (Linnaeus)—Common Muskrat

Formerly the muskrat did not occur south of the Arkansas River and the Ouachita Mountains (cf. A survey of Arkansas game, 1951). The Arkansas Game and Fish Commission has been carrying on a program of restocking for several years and muskrats are now nearly state wide in distribution, except for the extreme southeastern portion of the State. This species has been reported from forty-eight of seventy-five counties and seems to be extending its range southward at a fairly rapid rate, particularly in northeastern Arkansas, probably as the result of expansion of the rice industry and associated irrigation creating more favorable habitat.

Specimens examined.—UADZ, total 5. BENTON Co.: Springdale-(1); POINSETT Co.: Weiner-(3); WASHINGTON Co.:-(1).

Other records.—BENTON Co.: Elm Springs (2)—Dellinger and Black (1940); FRANKLIN Co.: Ozark—Black (1936); FULTON Co.: Mammoth Springs (2)—Dellinger and Black (1940), (4)—Hollister (1911); MADISON Co.: Huntsville—Black (1936); MISSISSIPPI Co.: Leachville—C. W. Nelson (*pers. comm.*); NEWTON Co.: Marble Falls (1)—G. Rush (*pers. comm.*); WASHINGTON Co.: Brentwood, Fayetteville, Winslow—Black (1936), Prairie Grove—O. Hite (*in. litt.*); reported from the following counties by personnel of the Arkansas Game and Fish Commission: Baxter; Boone; Carroll; Clay; Cleveland; Columbia; Conway; Craighead; Crawford; Crittenden; Cross; Garland; Hempstead; Hot Spring; Howard; Independence; Izard; Jackson; Lawrence; Lee; Logan; Lonoke; Marion; Nevada; Ouachita; Phillips; Pike; Polk; Pope; Prairie; Pulaski; Randolph; Saline; Searcy; Sebastian; Sharp; St. Francis; White; Woodruff; Yell.

Family MURIDAE

RATTUS NORVEGICUS (Berkenhout)—Norway Rat

The Norway rat is found in and near buildings in both urban and rural areas and is undoubtedly state wide in distribution.

Specimens examined.—UADZ, total 9. BENTON Co.: Rogers (1); CONWAY Co.: Morrilton (1); LONOKE Co.: Lonoke (2); WASHINGTON Co.: Fayetteville (5).

Other records.—JEFFERSON Co.: Pine Bluff—J. P. Redman (*in. litt.*); PERRY Co.: Bigelow (1)—H. Newman (*pers. comm.*).

RATTUS RATTUS ALEXANDRINUS (Geoffroy)—Roof Rat

The sole record for the State is one specimen from Delight, Pike County.

Specimens.—BS, total 1. PIKE Co.: Delight (1-BS).

MUS MUSCULUS Linnaeus—House Mouse

The house mouse occurs throughout the State. It is often captured in fields and brushy areas during the summer months but moves into buildings during colder weather. It is possible that the races *brevirostris* and *domesticus* are both represented in the State with a preponderance of the latter race. According to Lowery (1943) the two races may be at least partially segregated ecologically with *brevirostris* restricted to open situations and *domesticus* to dwelling places and their vicinity.

Specimens examined.—UADZ, total 28. BENTON Co.: 3 miles N Springdale (3); CONWAY Co.: Morrilton (2); CRAWFORD Co.: Alma (1); JEFFERSON Co.: Pine Bluff (3); LONOKE Co.: Lonoke (3); MISSISSIPPI Co.: Leachville (3); PERRY Co.: Bigelow (1), SEBASTIAN Co.: Fort Smith (1); UNION Co.: Calion (1), El Dorado (3); WASHINGTON Co.: Fayetteville (7).

Additional specimens.—total 28 plus. BENTON Co.: 8 miles E Siloam Springs (IU); SEBASTIAN Co.: Fort Smith (1-BS); WASHINGTON Co.: Fayetteville (1-BS); 8 miles W Springdale (1-IU), Winslow (24-KU); WHITE Co.: Beebe (1-BS).

Other records.—FRANKLIN Co.: Ozark—Black (1936); INDEPENDENCE Co.: Batesville—W. L. Henning (*in. litt.*); MADISON Co.: Huntsville—Black (1936); POLK Co.: Mena (1)—R. B. Loomis (*in. litt.*); POPE Co.: Russellville (4)—E. B. Holmes (*in. litt.*).

Family CAPROMYIDAE

MYOCASTOR COYPUS BONARIENSIS (E. Geoffroy-Saint-Hilaire)—Nutria

The first feral nutria caught in Arkansas was taken in a steel trap near a lily pond about 12 miles from Texarkana, Miller County, during the first

week of December 1953. The female specimen was sent to the Little Rock Zoo for exhibition. This animal may have escaped from a private pond or it might have emigrated into Arkansas from Louisiana where nutria have been feral since at least 1943 (Lowery, 1943). Nutrias were observed in northeast Miller County in both 1954 and 1955 and may have moved into adjacent Hempstead County from which this species was reported in March 1955. It has also been reported that a pair of nutria are located on a private lake in southwestern Sebastian County where the owner introduced them to control aquatic vegetation. Another nutria was trapped on November 30, 1954 at Dry Creek, near Wyatt School, about five miles southwest of El Dorado, Union County. This specimen may have been an escape as a farmer living 10 miles west of El Dorado reportedly introduced three pair of nutria from Louisiana into his private pond (A. J. Hoiberg, *in. litt.*, 1954). Another rather indefinite report of this animal was obtained by A. J. Hoiberg from Strong, Union County.

Records.—HEMPSTEAD CO.: Reported by E. J. Barham, 1955; MILLER CO.: Texarkana (1)—Arkansas Gazette, December 12, 1953; SEBASTIAN CO.: Reported by L. McBride, 1955; UNION CO.: El Dorado (1), Strong—A. J. Hoiberg (*in. litt.*).

Family CANIDAE

CANIS LATRANS FRUSTROR Woodhouse—Oklahoma Coyote

Coyotes are common in western Arkansas and a fairly large number of them are taken in the State every year by government trappers. This species seems to be moving eastward in the State with the cutting of the forests and creation of open lands (cf. A survey of Arkansas game, 1951). Unsubstantiated reports of coyotes have been obtained for Baxter, Fulton and Jackson counties. Perhaps the range in Arkansas now extends past the central portion of the State, although there is a possibility that the coyote has been confused with the red wolf which often is very similar in general appearance.

Specimens examined.—UADZ, total 7. BENTON CO.: 5 miles E Rogers (2); CALHOUN CO.: Near Calion (1); WASHINGTON CO.: Brentwood (1), Winslow (3).

Other records.—WASHINGTON CO.: Cincinnati (1), Fayetteville—Dellinger and Black (1940), Prairie Grove—O. Hite (*in. litt.*); reported from the following counties by Arkansas Game and Fish Commission personnel: Baxter; Carroll; Columbia; Crawford; Franklin; Fulton; Hempstead; Jackson; Madison; Pike; Yell.

CANIS NIGER GREGORYI Goldman—Mississippi Valley Red Wolf
CANIS NIGER RUFUS Audubon and Bachman—Texas Red Wolf

The smaller race *rufus*, which closely resembles the coyote in general characters, has been recorded from Madison, Newton, Pope, Stone, and Washington counties. None of the records is recent and this race is now believed to be restricted to parts of central and southern Texas. The race *gregoryi* occurs throughout the State and is quite numerous in some counties. It evidently has largely replaced the race *rufus* over its former range in Arkansas. Nearly 1400 wolves were reported taken in the State by the Predator and Rodent Control Program of the U. S. Fish and Wildlife Service in the period from 1951 through 1954. The Predator and Rodent Control Program does not distinguish between coyotes and wolves, but it is believed that the

majority of those taken, particularly in the more eastern counties, were of the species *C. niger*. In the fiscal year 1951 the Predator and Rodent Control Program reported taking 69 wolves from Crawford County alone. Some of the reported wolves were probably dog-wolf hybrids which are fairly common in Arkansas. More coyotes are undoubtedly included in the total from the western counties. A majority of the specimens examined by the writer have been in the black pelage phase with the typical white pectoral spot.

Specimens examined.—UADZ, total 10. DALLAS Co.: Carthage (2); LAWRENCE Co.: Imboden (1); LOGAN Co.: New Blain (1); MADISON Co.: Rockhouse (1); STONE Co.: State Game Refuge (1); WASHINGTON Co.: Brentwood (2), Strickler (2).

Additional specimens.—total 133. BOONE Co.: Bergman (2-USNM), Lead Hill (1-USNM); CHICOT Co.: 12 miles E Parkdale (1-USNM); CLARK Co.: Graysonia (1-USNM); CLEBURNE Co.: Almond (1-USNM); GARLAND Co.: Crystal Springs (1-USNM), Gladstone (1-USNM), 9 miles E Hot Springs (1-USNM), 6 miles W Lonsdale (4-USNM); GREENE Co.: Delaplaine (1-USNM); MADISON Co.: Redstar (1-USNM); MARION Co.: Mull (4-USNM), Rush (2-USNM); MILLER Co.: Garland (2-CNHM); NEWTON Co.: Boxley (2-USNM), Fallsville (9-USNM), Lurton (2-USNM); PERRY Co.: Aplin (1-USNM), Ava (3-USNM), Hollis (1-USNM), Thornburg (1-USNM), Wye (2-USNM); POLK Co.: Egger (7-USNM), Mena (1-USNM), Hartley (1-USNM), Potter (1-USNM), Shady (3-USNM); POPE Co.: Hector (1-USNM, Mill Creek (3-USNM), Raspberry (3-USNM), Simpson (6-USNM), Solo (1-USNM); PULASKI Co.: Ferndale (8-USNM), Maumelle Creek (1-USNM), Pinnacle (6-USNM); SALINE Co.: Isaac (6-USNM); SCOTT Co.: Blue Ball (4-USNM), Cardiff (1-USNM), Cedar (2-USNM), Parks (1-USNM); ST. FRANCIS Co.: Forrest City (1-USNM); STONE Co.: Fifty-six (4-USNM), Signal Hill (1-USNM); WASHINGTON Co.: Summers (7-USNM); YELL Co.: Aly (1-USNM), Onyx (11-USNM), Stillwater (8-USNM).

Other records.—CRAWFORD Co.: Schaberg—Dellinger and Black (1940); HOWARD Co.: Big Woods Game Refuge (2)—Dellinger and Black (1940); SEARCY Co.: St. Joe (1)—Dellinger and Black (1940); WASHINGTON Co.: Fayetteville (1), Summers (1)—Dellinger and Black (1940), Prairie Grove—O. Hite (*in. litt.*); reported by Arkansas Game and Fish Commission personnel from the following counties: Ashley; Baxter; Benton; Bradley; Calhoun; Carroll; Columbia; Franklin; Fulton; Grant; Hempstead; Hot Spring; Independence; Jackson; Johnson; Lafayette; Lincoln; Little River; Ouachita; Pike; Prairie; Sevier; Sharp.

VULPES FULVA (Desmarest)—Red Fox

The red fox is not native to Arkansas but has extended its range into the State from the North and has been introduced from the East and North into various parts of the State by sportsmen who consider them superior to the gray fox for hunting. This species is now well established in all but a few counties in the southeastern and southwestern corners of the State but is not nearly as numerous as the gray fox. Red foxes now in Arkansas are probably a mixture of the northern race *regalis* and the eastern race *fulva*.

Specimens examined.—UADZ, total 3. JEFFERSON Co.: Pine Bluff (2); WASHINGTON Co.: Durham (1).

Additional specimens.—total 1. BOONE Co.: Keener (1-MVZ).

Other records.—SEBASTIAN Co.: Monte Vista (1)—Lyndal York (*in. litt.*); WASHINGTON Co.: Prairie Grove (1)—Dellinger and Black (1940), West Fork—Dellinger and Black (1940), Winslow (1)—Black (1936), (1)—Dellinger and Black (1940); reported by Arkansas Game and Fish Commission personnel from the following counties: Ashley; Baxter; Benton; Calhoun; Carroll; Chicot; Clark; Clay; Cleburne; Cleveland; Columbia; Crawford; Crittenden; Cross; Dallas; Franklin; Fulton; Garland; Hempstead; Hot Spring; Howard; Independence; Izard; Jackson; Johnson; Lawrence;

Lee; Lincoln; Lonoke; Madison; Marion; Mississippi; Monroe; Nevada; Ouachita; Perry; Phillips; Pike; Poinsett; Polk; Prairie; Randolph; Scott; Searcy; Sevier; Sharp; Union; Woodruff; Yell.

UROCYON CINEREOARGENTEUS OCYTHOUS Bangs—Wisconsin Gray Fox

Gray foxes are very numerous throughout the State and rank fifth among furbearers in total value of pelts and in numbers trapped (cf. A survey of Arkansas game, 1951).

Specimens examined.—UADZ, total 14. BENTON CO.: Bella Vista (1), Gravette (1); GARLAND CO.: (1); MADISON CO.: Hindsville (1); WASHINGTON CO.: Fayetteville (1), West Fork (8), Winslow (1).

Additional specimens.—total 1. UNION CO.: El Dorado (1-AJH).

Other records.—CARROLL CO.: Berryville (2)—Dellinger and Black (1940); JEFFERSON CO.: 12 miles SE Altheimer (1)—R. G. Leonard (*pers. comm.*), Pine Bluff (1)—J. P. Redman (*pers. comm.*); WASHINGTON CO.: Fayetteville (1)—Dellinger and Black (1940), Winslow (1)—Black (1936), Prairie Grove—0. Hite (*in. litt.*); reported from the following counties by Arkansas Game and Fish Commission personnel: Ashley; Baxter; Boone; Bradley; Calhoun; Chicot; Clark; Clay; Cleburne; Cleveland; Columbia; Crawford; Crittendon; Cross; Dallas; Fulton; Hempstead; Hot Spring; Howard; Independence; Izard; Johnson; Lawrence; Lee; Lincoln; Lonoke; Marion; Mississippi; Monroe; Nevada; Ouachita; Perry; Phillips; Pike; Poinsett; Polk; Prairie; Randolph; Scott; Searcy; Sevier; Sharp; Woodruff; Yell.

Family URSIDAE

URSUS AMERICANUS AMERICANUS Pallas—American Black Bear
URSUS AMERICANUS LUTEOLUS (Griffith)—Louisiana Black Bear

Bears were formerly so numerous in Arkansas that it was unofficially called "The Bear State." Bear hunting has been illegal in the State since 1927 when the season was closed. A few bears are still killed illegally but there is some evidence that they are slowly increasing in numbers in areas where they were not completely exterminated. The latest official estimate (cf. A survey of Arkansas game, 1951) placed the bear population in the State at between 40 to 50. More than half the bear population is concentrated in and around the White River National Wildlife Refuge in Monroe, Arkansas, and Desha counties and along the Mississippi bottoms as far north as Lee and Monroe counties. The remainder of the bear population is scattered through the Ouachita Mountains and in parts of the Ozarks. A pair of bears was introduced into Stone County by the Arkansas Game and Fish Commission in 1949. One was shot shortly after being released. Bear sign has been located in Baxter and Stone counties in 1951 (T. H. Holder, *in litt.*) and in Stone County in 1955 (C. J. Perkins, *in. litt.*). Evidently more bears are present in this area of the Ozarks than the one released. A 90-pound bear was captured west of Harrison near Alpena in Boone County by E. O. Thomason and S. A. Dyer on June 16, 1950. Another was captured near Harrison, Boone County, in 1953. Two bears were observed near Silver Hill, Searcy County, in 1951, and another was observed north of Pindall on the Newton-Searcy County line in 1955 (H. B. Hensley, *in. litt.*). A bear was observed near Landis, Searcy County by H. Lawrence, postmaster at Landis, and bear tracks were noticed by Fred Bell and H. B. Hensley near the mouth of

Cave Creek on the Buffalo River (H. B. Hensley, *in. litt.*, 1953). A bear was also observed in Fulton County in 1952.

Bear sign, though not recent, was reported from Benton and Washington Counties (Black, 1936; Dellinger and Black, 1940). Two bears were planted in the Black Mountain Refuge, Franklin County, by the Arkansas Game and Fish Commission in 1949. Signs have been observed by hunters as recently as 1955 but no actual sight records have been obtained.

Bears and bear signs have been reported from a number of counties in the Ouachita Mountain Region, the West Gulf Coastal Plain Region and the Mississippi Alluvial Plain. A 350-pound bear was shot near Delco Lake, Desha County, on June 17, 1951. Another was seen in the White River bottoms, 11 miles north of Watson, Desha County, by V. O. Johnson in December 1952 (R. D. Norris, *in. litt.*). Bears have also been observed quite frequently in the bottoms around Escronges Lake, Essex Bayou, and Scrub Grass Bayou in Arkansas County and in the vicinity of Half Moon Lake and Big Island in Desha County. In Phillips County bears have been observed most often in the White River bottoms from the mouth of Big Creek to the Desha-Phillips County line. One small bear was observed by R. D. Norris in the east-central part of Lincoln County in 1954. Another was observed by E. D. Hill in the southern part of Perry County in August 1952.

The majority of the bear population in the State at present, which is concentrated in the bottoms of the White and Mississippi rivers in southeastern Arkansas, probably belongs to the race *luteolus*. The bears now found in northern and western parts of the State are probably referable to the nominate race on the basis of geographic distribution.

Records.—ARKANSAS CO.: Scrub Grass Bayou (1)—Dellinger and Black (1940), Escronges Lake, Essex Bayou, north of Nady—Carl Hunter (P-R Project 11-R, 1945); BENTON CO.: 6 miles E Lowell-Tracks—Black (1936); BOONE CO.: Alpena (1), 1950—A. Auman (*in. litt.*), Harrison (1)—Arkansas Gazette (Sept. 20, 1953); DESHA CO.: Watson (1)—N. W. Arkansas Times (June 19, 1951), 11 miles N Watson, 1952—R. D. Norris (*in. litt.*), Scrub Grass Bayou, Half Moon Lake, Big Island, Stimson (6-10) estimated—Roy Wood (P-R Project 11-R, 1945); LINCOLN CO.: (1)—R. D. Norris (*in. litt.*); MONROE CO.: Holly Grove (1), 1927—Dellinger and Black (1940); PHILLIPS CO.: White River bottoms, 10 estimated—Roy Wood (P-R Project 11-R, 1945); SEARCY CO.: Landis, Silver Hill, north of Pindall—E. B. Hensley (*in. litt.*); WASHINGTON CO.: White River bluffs—Dellinger and Black (1940); reported from the following counties by Arkansas Game and Fish Commission personnel: Baxter; Bradley; Chicot; Clark; Columbia; Franklin; Fulton; Jefferson; Lee; Montgomery; Ouachita; Perry; Polk; Saline; Stone; Yell.

Family PROCYONIDAE

PROCYON LOTOR VARIUS Nelson and Goldman—Alabama Raccoon
PROCYON LOTOR HIRTUS Nelson and Goldman—Upper Mississippi Valley Raccoon

Raccoons are found throughout the State and are very numerous in some localities. In general, the raccoon population appears to be increasing in Arkansas. Since 1942 the Arkansas Game and Fish Commission has trapped and released a large number of raccoons in various parts of the State and this program has without doubt contributed to the population increase. Rac-

coons are somewhat more abundant in forested bottomlands in close proximity to water. This species is an important furbearer and usually ranks about second in numbers trapped in the State.

Most of the raccoons in the State seem to be referable to the race *hirtus*, although two specimens from Randolph and Poinsett counties agree in general characteristics with the race *varius*. There is a possibility that the race *fuscipes* may occur in the extreme southwestern corner of the State but no specimens have been examined from that area. Melanistic and albinistic raccoons are fairly frequent in occurrence and the cinnamon color phase appears occasionally.

Specimens examined.—UADZ, total 2. POINSETT CO.: Weiner (1); RANDOLPH CO.: Dalton (1).

Additional specimens.—total 4. BOONE CO.: Zinc (1-MVZ); DESHA CO.: Big Island (2-ASM); STONE CO.: Marcella (1-CNHM).

Other records.—BENTON CO.: War Eagle (1)—Dellinger and Black (1940); CONWAY CO.: Morrilton (1)—W. Britt (*pers. comm.*); JEFFERSON CO.: Pine Bluff—J. P. Redman (*pers. comm.*); PERRY CO.: Bigelow (2)—H. Newman (*pers. comm.*); SEBASTIAN CO.: Monte Vista (1)—Lyndal York (*in. litt.*); UNION CO.: Calion—A. J. Hoiberg (*in. litt.*); WASHINGTON CO.: Fayetteville (1), Goshen (2), West Fork (1)—Dellinger and Black (1940), Prairie Grove—O. Hite (*in. litt.*); reported from remaining counties in the State by personnel of the Arkansas Game and Fish Commission.

Family MUSTELIDAE

MUSTELA FRENATA PRIMULINA Jackson—Missouri Weasel

This is the only weasel found in Arkansas. Although quite uniformly distributed over the State, it is rare or scarce in most areas. The race *primulina* closely resembles the race *noveboracensis* and intergradation between these two races, as well as with the races *spadix, arthuri,* and *longicauda,* occurs quite frequently (Hall, 1951).

Specimens examined.—UADZ, total 4. ARKANSAS CO.: Wrape Plantation, Bayou Meto (1); COLUMBIA CO.: Magnolia (1); JEFFERSON CO.: Pine Bluff (1); WASHINGTON CO.: Fayetteville (1).

Additional specimens.—total 18. BOONE CO.: Bergman (17-MVZ); SEBASTIAN CO.: Fort Smith (1-USNM).

Other records.—CRAWFORD CO.: Winslow (1)—Black (1936); FRANKLIN CO.: Ozark—Black (1936); MADISON CO.: Huntsville—Black (1936); NEWTON CO.: Marble Falls—Dellinger and Black (1940); WASHINGTON CO.: Fayetteville, Winslow—Black (1936), Dellinger and Black (1940); reported from the following counties by Arkansas Game and Fish Commission personnel: Ashley; Baxter; Benton; Bradley; Carroll; Chicot; Clay; Cleburne; Cleveland; Crittenden; Cross; Dallas; Fulton; Garland; Hempstead; Hot Spring; Independence; Izard; Jackson; Lawrence; Lonoke; Marion; Mississippi; Monroe; Perry; Phillips; Poinsett; Prairie; Randolph; Searcy; Sharp; Union; Woodruff; Yell.

MUSTELA VISON MINK Peale and Palisot de Beauvois—Large Brown Mink

Minks are found throughout Arkansas. In the last two or three years, 1952 to 1954, they seem to have increased in numbers in many areas of the State and are considered very common in many of the eastern and south-central counties. Low points in the mink population were reached in 1935 and 1946 (cf. A survey of Arkansas Game, 1951). The increased mink population at present to some extent may be coincident with an increase in the muskrat

population. A few mink have been trapped and released in State game refuges by employees of the Arkansas Game and Fish Commission. There is a possibility that intermediates between the races *mink* and *letifera* may occur in northwestern Arkansas and between the races *mink* and *vulgivaga* in southeastern Arkansas, but too few specimens are available to draw any taxonomic conclusions.

Specimens examined.—UADZ, total 5. BENTON CO.: Cave Springs (1); LOGAN CO.: Paris (1); RANDOLPH CO.: (1—skull); WASHINGTON CO.: Elm Springs (1); WOODRUFF CO.: Augusta (1).

Additional specimens.—total 4. BOONE CO.: Bergman (3-MVZ); DESHA CO.: Big Island (1-ASM).

Other records.—CONWAY CO.: Morrilton (3)—W. Britt (*pers. comm.*); FRANKLIN CO.: Alix (1)—Black (1936); MADISON CO.: Huntsville—Black, 1936); PERRY CO.: Bigelow (2) H. Newman (*pers. comm.*); UNION CO.: Smackover (1)—A. J. Hoiberg (*in. litt.*); WASHINGTON CO.: Prairie Grove—O. Hite (*in. litt.*), West Fork, Winslow—Black (1936); reported from remaining counties in State (with exception of Arkansas, Clay, Craighead, Faulkner, Grant, Greene, Lafayette, Little River, Miller, Montgomery, Pope, Pulaski, Saline, Sebastian, Stone, Van Buren and White counties) by personnel of the Arkansas Game and Fish Commission.

SPILOGALE INTERRUPTA (Rafinesque)—Prairie Spotted Skunk

Spotted skunks, or civet cats, are fairly common in the prairie areas of western Arkansas and in the Grand Prairie area in eastern Arkansas. This species is apparently nearly state wide in distribution and is locally common in several counties in eastern Arkansas which they have apparently invaded in the last few years. Dellinger and Black (1940) gave the apparent eastern limit for the State as Hot Springs, Garland County, but this species was evidently well established in parts of eastern Arkansas even then.

Specimens examined.—UADZ, total 4. RANDOLPH CO.: Dalton (1); WASHINGTON CO.: (1), Fayetteville, Lake Wedington Area (1).

Additional specimens.—total 5. BOONE CO.: Bergman (1-MVZ), Olney (1-MVZ), Zinc (1-MVZ); SEBASTIAN CO.: Fort Smith (2-MVZ).

Other records.—GARLAND CO.: Hot Springs—Dellinger and Black (1940); NEWTON CO.: Marble Falls (1)—Dellinger and Black (1940); WASHINGTON CO.: Brentwood (20)—Black (1936), Prairie Grove—O. Hite (*in. litt.*), Sulphur City (1)—Dellinger and Black (1940); reported from the following counties by Arkansas Game and Fish Commission personnel: Arkansas; Ashley; Baxter; Bradley; Chicot; Cleburne; Cross; Dallas; Franklin; Fulton; Hempstead; Hot Spring; Howard; Independence; Izard; Jackson; Lawrence; Lonoke; Madison; Marion; Nevada; Perry; Phillips; Pike; Polk; Prairie; Searcy; Sevier; Sharp.

MEPHITIS MEPHITIS MESOMELAS Lichtenstein—Louisiana Skunk

This species is an important furbearer, ranking third in numbers caught, in Arkansas. It is state wide in distribution and is very common in the Grand Prairie area and in the bottomlands of eastern Arkansas. The Louisiana skunk is also numerous in some of the upland areas in the Ozarks and the Ouachita Mountains.

Specimens examined.—UADZ, total 7. BOONE CO.: Marble Falls (1); RANDOLPH CO.: Dalton (1); WASHINGTON CO.: (4); Fayetteville (1).

Additional specimens.—total 12. BOONE CO.: (4-MVZ), Bergman (7-MVZ); POLK CO.: Rich Mountain (1-BS).

Other records.—BOONE Co.: Harrison (3)—Dellinger and Black (1940); CRAWFORD Co.: Alma (1)—C. W. Nelson (*pers. comm.*); JEFFERSON Co.: 20 miles SE Altheimer (3)—R. G. Leonard (*pers. comm.*), Pine Bluff—J. P. Redman (*pers. comm.*); reported from the following counties by Arkansas Game and Fish Commission personnel: Arkansas; Ashley; Baxter; Benton; Bradley; Calhoun; Carroll; Chicot; Clark; Clay; Cleburne; Cleveland; Columbia; Crittenden; Cross; Dallas; Franklin; Fulton; Garland; Hempstead; Hot Spring; Howard; Independence; Izard; Jackson; Lawrence; Lee; Lincoln; Lonoke; Madison; Mississippi; Nevada; Ouachita; Perry; Phillips; Pike; Poinsett; Pope; Prairie; Scott; Searcy; Sevier; Sharp; St. Francis; Union; Woodruff; Yell.

LUTRA CANADENSIS INTERIOR Swenk—Interior Otter

It has been estimated that there are probably between 700 and 800 otters in the State (cf. A survey of Arkansas Game, 1951). Otters are found in more than 40 counties in Arkansas, but occur principally in the central and eastern parts of the State. They are especially numerous in the alluvial plain along the Mississippi River where they are found on the White, Cache, St. Francis, Saline and Black rivers. In 1955 otters were reported to be so abundant on Tulip Creek, Bayou Freeo; Ouachita River and Saline River in Dallas and Ouachita counties that residents in the area were becoming very concerned about their effect on fishing. There are few otter in western Arkansas, although they have been observed along the lower Cossatot River and on Half-Moon Lake in Sevier County and on Little River in Hempstead County. In 1948 an otter was killed five miles west of Centerton in Benton County at a distance of about two miles from the nearest water. A sight record was reported on Spavinaw Creek, near Gravette, Benton County, by Dellinger and Black (1940). These are the only otter records from northwestern Arkansas. The otter population in the State appears to be increasing slowly and otters now are seen frequently in areas where they were once near extinction.

Specimens examined.—UADZ, total 2. LAWRENCE Co.: Sedgewick (1); PHILLIPS Co.: Helena (1).

Additional specimens.—total 2. DESHA Co.: Big Island (2-ASM).

Other records.—BENTON Co.: Centerton (1), J. Bagget (*in. litt.*), Gravette (1)—Dellinger and Black (1940); DREW Co.: Monticello—Dellinger and Black (1940); POPE Co.: Big Piney Creek (1)—Dellinger and Black (1940); SHARP Co.: Spring River (1)—A survey of Arkansas game (1951); UNION Co.: Ouachita River—A. J. Hoiberg (*in. litt.*); reported from the following counties by Arkansas Game and Fish Commission personnel: Arkansas; Ashley-Saline River, Bayou Bartholomew; Bradley-Moro Creek; Calhoun; Chicot; Clay-Black River; Cleveland-Saline River; Crittenden; Dallas-Tulip Creek, Saline River; Garland; Green-Cache River, St. Francis River; Hempstead-Little River; Hot Spring; Independence; Jackson; Jefferson; Lee-Big Creek, L'Anguille River, McAnulty Lake, St. Francis River; Lincoln-Bayou Bartholomew; Lonoke-Bayou Meto; Mississippi-Big Lake; Monroe; Ouachita; Perry-Big Bull Lake, Little Lake; Poinsett-Bayou De View; Prairie; Randolph; Sevier-Cossatot River, Half-Moon Lake; Van Buren-Little Red River; Woodruff; Yell-Petit Jean River.

Family FELIDAE

FELIS CONCOLOR CORYI Bangs—Florida Puma

The puma supposedly became extinct in Arkansas about 1920 when the deer population in the State was at a low ebb. A number of sight records accumulated since about 1945 and one recorded kill in Montgomery County

in 1949 (Sealander, 1951) seem to indicate that this species never was completely exterminated in Arkansas, although it was almost at the vanishing point. With a rise in the deer population there seems to have been an increase in the mountain lion population in Arkansas, based on frequency of reports, many of which are very reliable. Most of the pumas have been reported from locations in or near the heaviest deer concentrations in the State.

Mrs. O. B. Witherspoon and Mrs. Pierre Redman of Mena, Polk County, saw a grown puma cross the road near Eagleton in the fall of 1946. Mrs. Witherspoon also saw a full grown puma with two juveniles crossing the road on several occasions in 1945 and 1946 in the vicinity of Acorn and Eagleton. J. P. Redman (*pers. comm.*) also sighted a puma during mid-November 1949 between Shady Community and the Shady Lake Recreational Area. State trapper T. N. Rush (*pers. comm.*) observed tracks on several occasions in Izard County in 1952 and reports sight observations by several people in the county in the same year. During the first week in March 1953 a puma was observed on the Johnson ranch between Ash Flat and Hardy, Sharp County. Mr. Rush reported that a calf was killed on this ranch which showed very evident signs of a mountain lion kill. Another puma was reported from the Ruddell Bottom section near Batesville, Independence County in December 1953 by Henry Wood of Ruddell Hill. Members of a Missouri Pacific section crew found mountain lion tracks near Cushman Junction, two miles north of Batesville in December 1953. State trapper O. L. Cardin (*in litt.*) observed a puma on December 31, 1953 in the Cooper Bottoms about eight miles southwest of Malvern, Hot Spring County. He was able to approach to within about 50 yards of the cat and observed it as it made approximately a 24-foot jump across the road. About a week later Mr. Cardin reported that a large buck deer was killed by a lion about 15 miles north of Cooper Bottoms. The carcass was carried for a distance of around 35 yards, placed in a deep gully and covered with leaves. Mr. Cardin observed lion tracks in Hot Spring County again in October 1954. Another puma was observed by Mr. and Mrs. W. W. Barnett between Humnoke and Stuttgart, Lonoke County, on January 18, 1954. Several reports of mountain lions have also been received from northwestern Arkansas, although the majority may be unreliable. Mr. Harold Alexander of the Arkansas Game and Fish Commission reports that a mountain lion was observed near Cass, Franklin County, in November 1954 by a reliable hunter who hunts yearly in New Mexico and other western states and is thoroughly familiar with the cougar. Another seasoned western hunter, Mr. W. M. Elvins of Fayetteville, Washington County, reported (pers. comm.) that he saw a full grown puma cross the road near his farm located 11 miles southeast of Fayetteville and 5 miles east of Greenland in October 1954. He also observed tracks around a pond and in an old road near his farm in January 1955. His neighbor, a Mr. H. Wallen, is reported to have observed a mountain lion one or two miles north of Mr. Elvin's farm in January 1955.

Tracks and other signs of mountain lions have been reported from Bradley, Clark, Cleveland, Garland, Miller, and Ouachita counties but no sight records have been obtained.

Specimens examined.—None.

LYNX RUFUS RUFUS (Schreber)—Eastern Bobcat
LYNX RUFUS FLORIDANUS Rafinesque—Florida Bobcat

Bobcats are common in many Arkansas counties and have been reported from every county in the State. A considerable number are trapped every year in various parts of the State by the Predator and Rodent Control branch of the U. S. Fish and Wildlife Service. The race *floridanus* occupies most of eastern Arkansas (Peterson and Downing, 1952) while the nominate race is found in western Arkansas. Presumably a zone of intergradation between the two races occurs across central Arkansas. In some counties a large number of those specimens trapped show varying degrees of melanism.

Specimens examined.—UADZ, total 11. CLARK CO.: Arkadelphia (1), Graysonia (2); GARLAND CO.: (1); HOWARD CO.: Umpire (1); MADISON CO.: Rockhouse (1); POPE CO.: Russellville (1); PULASKI CO.: Maumelle (1); SCOTT CO.: Black Fork Mountain (2).

Additional specimens.—total 30. DESHA CO.: Big Island (3-ASM).

Other records.—BOONE CO.: Marble Falls (2)—Dellinger and Black (1940); CRAWFORD CO.: Winslow (1)—Black (1936); FRANKLIN CO.: Cass (1)—Dellinger and Black (1940); NEWTON CO.: Jasper (2-stomachs examined by writer); WASHINGTON CO.: Prairie Grove—O. Hite (*in. litt.*); reported from remaining counties in State by Arkansas Game and Fish Commission personnel and by the Predator and Rodent Control branch of the U. S. Fish and Wildlife service.

Family CERVIDAE

CERVUS CANADENSIS NELSONI Bailey—Rocky Mountain Elk

The original elk, belonging to the nominate race, native to Arkansas were probably exterminated by about 1840. The elk now present in the State were introduced in 1933 by the U. S. Forest Service from the Wichita Mountains Wildlife Refuge in Oklahoma. The herd which originally numbered three bulls (one died shortly after release) and eight cows has increased slowly and now is estimated at approximately 200 head. Most of the herd is concentrated in the Black Mountain Refuge in Franklin County. Wanderers from the main herd have occasionally been reported from Washington, Madison, and Johnson counties.

Specimens examined.—None.

ODOCOILEUS VIRGINIANUS subspecies—White-tailed Deer

White-tailed deer which were originally abundant in Arkansas reached a low point of less than 500 head in 1927 (A survey of Arkansas game, 1951; Donaldson, Hunter and Holder, 1951; Alexander, 1954). An upswing in the population began with the establishment of refuges in 1926-27 and the importation of deer from other states. Deer are now present in every county in Arkansas and some areas of the State have actually become overpopulated. It is estimated that there may be over 60,000 deer in Arkansas at the present time. The deer herd now present in the State is probably a mixture of several races as the result of introductions from other states and the restocking program carried on by the Arkansas Game and Fish Commission in which deer have been trapped and moved from one area of the State to another. The original white-tails in Arkansas probably belonged largely to the race *macrourus*.

The races *borealis, virginianus, macrourus* and possibly *texanus* have been introduced from Wisconsin, North Carolina, Louisiana, and Texas.

Specimens examined.—UADZ, total 3. SEBASTIAN CO.: Fort Smith (1-skull); YELL CO.: Fourche Mountains (2).

Additional specimens.—total 1. DESHA CO.: Big Island (1-ASM).

Other records.—For records from remaining counties in State see Alexander (1954), Donaldson, Hunter and Holder (1951), and A survey of Arkansas game (1951).

Family BOVIDAE

BISON BISON BISON (Linnaeus)—Buffalo

Buffalo were last recorded in the State by Gerstaecker in 1837. They probably became extinct shortly thereafter. The last herd in the State was killed in 1808. The only buffalo now in Arkansas are captives introduced from other states.

Specimens examined.—None.

Hypothetical List

The mammals listed below include those which are likely to be found in the State with more intensive collecting.

1. *Lasionycteris noctivagans* (Le Conte) Silver-haired Bat.—This bat is very likely to be found in Arkansas in late spring and early autumn but may be absent in summer when it is resident in more northern states.

2. *Tadarida mexicana* (Saussure) Mexican Free-tailed Bat.—Systematic collecting in southwestern and western Arkansas should eventually locate this species which has been recorded from northeastern Texas and eastern Oklahoma. It is possible that the species *T. molossa* which ranges as far north as Iowa may also occur in Arkansas.

3. *Spermophilus tridecimlineatus pallidas* J. A. Allen. Thirteen-lined ground squirrel.—This species may occur in the prairie areas of extreme northwestern Arkansas. S. C. Dellinger (*pers. comm.*) has stated that he has observed this species on at least two occasions in Benton and Washington counties. Records have been obtained from northeastern Oklahoma and southwestern Missouri, so that this species presumably may occur to a limited extent in Arkansas. No specimens have yet been trapped or killed in the State.

4. *Spermophilus franklinii* (Sabine) Franklin Ground Squirrel.—J. D. Black (*in. litt.*, 1951) reports that he saw this species twice near Huntsville, Madison County. Both specimens were observed at very close range and Black states that he was positive in his identification. The writer on one occasion obtained a glimpse of what appeared to be this species near Goshen, Washington County, but was unable to get a close view to make positive identification.

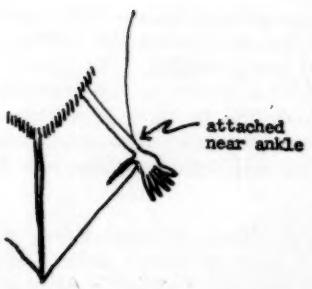
5. *Perognathus hispidus spilotus* Merriam. Hispid Pocket Mouse.—Glass (1947) states that this species occurs in the Red River Valley of Texas. On geographic grounds it should also occur in the Red River Valley in the extreme southwestern corner of Arkansas.

6. *Microtus ochrogaster ochrogaster* (Wagner) Prairie Vole.—A. H. Howell collected a specimen (in U.S. Biological Surveys collection) at Stuttgart, Arkansas County, in 1910 which he referred to this species. The specimen consisting of an incomplete skull is too youthful to permit accurate identification (E. R. Hall, *in. litt.*) and is probably referable to *Microtus pinetorum* on geographic grounds. The species *Microtus ochrogaster* should occur, however, in extreme northeastern Arkansas but no specimens from that area of the State have been collected.

7. *Zapus hudsonius pallidus* Cockrum and Baker. Hudsonian Jumping Mouse.—This species has been taken by B. P. Glass in Adair County, Oklahoma which lies adjacent to Washington and Crawford coutnies in Arkansas. Presumably it should occur on the western edge of Arkansas as well as in eastern Oklahoma.

GENERAL KEY TO SPECIES OF ARKANSAS MAMMALS

1.	Body almost completely enclosed in bony shell; teeth peg-like, 32 ..... *Dasypus novemcinctus*	
1′.	Body not enclosed in bony shell	2
2.(1′)	Forelimbs modified to serve as wings	3
2′.	Forelimbs not modified to serve as wings	14
3.(2)	Ears very long, usually about 30 mm or more; with a prominent fleshy lump above each nostril; three lower premolars on each side; teeth 36	4
3′.	Ears shorter, usually less than 20 mm; no lump above nostrils	5
4.(3)	Hairs on belly white-tipped; ears joined in middle; back cinnamon-brown; fur distinctly bi-color ..... *Corynorhinus rafinesquii*	
4′.	Hairs on abdomen buff-tipped; ears joined across forehead; back clove-brown; fur not distinctly bi-color ..... *Corynorhinus townsendii*	
5.(3′)	Dorsal surface of interfemoral membrane completely furred to tip of tail	6
5′.	Dorsal surface of interfemoral membrane naked except for scattered hairs, or furred only at extreme base or on basal one-third or one-fourth	7
6.(5)	Length of forearm less than 44 mm; total length less than 120 mm; general coloration bright rufous to yellowish-red or rich mahogany-brown ..... *Lasiurus borealis*	
6′.	Length of forearm more than 44 mm; total length more than 120 mm; general coloration yellowish-gray to grizzled brown, throat yellow ..... *Lasiurus cinereus*	
7.(5′)	Interfemoral membrane naked or furred at extreme base only	8
7′.	Interfemoral membrane slightly furred on basal one-fourth or one-third; yellowish-brown; wing membranes black; total length less than 90 mm; forearm 36 mm or less; teeth 34 ..... *Pipistrellus subflavus*	
8.(7)	Wing membrane attached to foot near ankle (fig. 2) and not at base of toes; hairs on back uniform in color from base to tips; dull brown to mouse gray; hairs on belly bi-color; teeth 38 ..... *Myotis grisescens*	
8′.	Wing membrane attached to foot at base of toes (fig. 3); hairs on back not uniformly colored from base to tip	9
9.(8′)	Length of forearm less than 40 mm	10
9′.	Length of forearm 40 mm or more; large, total length usually more than 105 mm; sepia-brown; hairs darker at base than tips; teeth 32 ..... *Eptesicus fuscus*	



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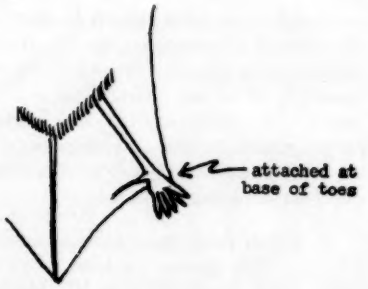

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10.(9) Tragus slender, pointed, more than 4 mm in length; ears usually pointed; two upper incisors on each side 11

10'. Tragus rounded, blunt, end curved inward, less than 4 mm in length; ears rounded, thick and leathery; membranes black; dull brown to chocolate-brown; one upper incisor on each side; teeth 30 ..... *Nycticeius humeralis*

11.(10) Ears when laid forward in normal position extend beyond tip of muzzle; back brownish-olive; membranes grayish; fur on back woolly or fuzzy in appearance ..... *Myotis keenii*

11'. Ears when laid forward in normal position do not extend beyond tip of muzzle; teeth 38 12

12.(11') Calcar with small but usually definite keel (fig. 4); hairs on back tri-colored; sometimes giving a pinkish-gray tinge to pelage; upper parts generally dark brown to blackish ..... *Myotis sodalis*

12'. Calcar long, usually without definite keel (fig. 5); hairs on back bi-colored; least width of interorbital constriction 4 mm or more 13

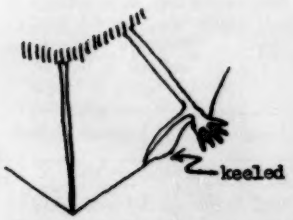
13.(12') Hairs on back with long glossy tips giving a somewhat metallic sheen to pelage; fur on back dense, not woolly, dull brown; hairs on belly buff-tipped; sagittal crest absent or indistinct ..... *Myotis lucifugus*

13'. Hairs on back without long glossy tips; fur on back dense, woolly, dull yellowish-brown; hairs on belly long, white-tipped; low but evident sagittal crest present ..... *Myotis austroriparius*

14.(2') Toes terminating in claws, not hooves 15

14'. Toes terminating in hooves, not claws 61

15.(14) Inner toe of hind foot thumb-like and clawless; tail naked, scaly and prehensile, black at base, white on distal half or more; female with external abdominal pouch; brain case very small with pronounced sagittal crest;



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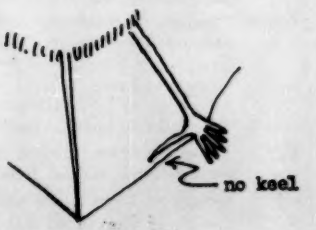

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palate perforated in addition to incisive foramina; ten upper incisors; teeth 50 ..... *Didelphis marsupialis*

15′. Inner toe of hind foot not thumb-like and clawed; fewer than ten upper incisors; tail variable but not prehensile 16

16.(15′) Toes on front foot five (first toe sometimes reduced and high on inside of foot); thumb always a claw, never a mere knob with a nail; canine teeth present; no diastema 17

16′. Toes on front foot usually only four (thumb sometimes present as a small knob with a nail); no canine teeth present; diastema present 33

17.(16) Total length less than 200 mm; snout elongated and pointed; eyes and external ears but little developed; fur velvety; canines usually undifferentiated and smaller than adjoining teeth; molar teeth with sharply pointed cusps with a distinct "W" pattern; zygomatic arches weak or absent 18

17′. Total length more than 200 mm; snout greatly elongated; eyes and external ears well developed; tail well haired; canines distinct and larger than incisors 21

18.(17) No ear pinna present; forefeet nearly as broad as long, modified for digging; total length more than 150 mm; weak zygomatic arches present; teeth 36, not tipped with brown ..... *Scalopus aquaticus*

18′. Ear pinna present; forefeet longer than broad; mouselike in appearance; total length less than 150 mm; zygomatic arches absent; teeth less than 36, tipped with orange or brown 19

19.(18′) Total length less than 82 mm; brownish; only three unicuspids visible from side view (fig. 6), fourth unicuspid minute and not visible from side; teeth 30, tipped with brown ..... *Cryptotis parva*

19′. Total length more than 88 mm; grayish 20

20.(19′) Ear protrudes conspicuously beyond fur; hind foot less than 11 mm; tail bi-colored, usually more than 25 mm; three unicuspids on each half of upper jaw, visible from side (fig. 7); teeth 28, tipped with orange..... *Notiosorex crawfordi*

20′. Ear does not protrude conspicuously beyond fur; hind foot 11 mm or more; tail not bi-colored, usually less than 24 mm; five unicuspids on each half of upper jaw, fifth unicuspid not visible from side (fig. 8); teeth 32, tipped with dark brown ..... *Blarina brevicauda*

21.(17′) Size very large, weight 200-500 pounds; tail short and concealed in long fur of rump; three molar teeth in each jaw; length of skull more than 250 mm ..... *Ursus americanus*

21′. Size small to medium, weight less than 100 pounds; tail conspicuous, not concealed in fur; two lower molar teeth in each jaw; length of skull less than 250 mm 22

22.(21′) Five claws on both front and hind feet 23

22′. Four claws on hind foot, five claws on front foot (first toe reduced and high on foot) 28

23.(22) Tail with series of buff and black rings with tip black; horizontal black mask across forehead and eyes; teeth 40, last molar wider than long..... Procyon lotor

6 7 8

23′. Tail without series of rings; no black mask across forehead and eyes; teeth less than 40 24

24.(23′) Toes completely webbed; total length more than 800 mm; tail more than 250 mm, noticeably thickened at base; five cheek teeth on each side of upper jaw ..... *Lutra canadensis*

24′. Toes not webbed; total length less than 800 mm; four cheek teeth on each side of upper jaw 25

25.(24′) Body elongate; legs short; without conspicuous markings on back or head; claws partially retractile; males larger than females; median lobe of bony palate extends appreciably beyond posterior edges of last upper molars; last upper molar almost triangular 26

25′. Body not elongate; with conspicuous markings of contrasting black and white on back, face, or head; claws not retractile; median lobe of bony palate terminates at or only slightly beyond posterior edges of last molars; last upper molar squarish 27

26.(25) Length more than 500 mm; uniformly dark brown above and below, except for occasional white pectoral spotting, at all seasons; skull about 70 mm long ..... *Mustela vison*

26′. Length less than 500 mm; underparts white or washed with yellowish; upperparts brown; tail tipped with black; skull less than 55 mm long ..... *Mustela frenata*

27.(25′) Black with short, narrow, white dorsal stripes ..... *Mephitis mephitis*

27′. Black with white patch on forehead and with four or more lines of broken stripes or spots ..... *Spilogale interrupta*

28.(22′) Claws blunt and not retractile; elongated muzzle; tail bushy; two upper molars in each jaw; teeth 42 29

28′. Claws short, sharp and retractile, concealed in fur; short muzzle; tail not bushy; one upper molar in each jaw; teeth 30 or 32 32

29.(28) Tail to tip of last vertebrae more than half as long as head and body; length less than 1050 mm; hind foot less than 160 mm 30

29′. Tail to tip of last vertebrae less than half as long as head and body; length more than 1200 mm; hind foot more than 160 mm 31

30.(29) Upper parts grizzled-grayish; legs and feet reddish-brown; outer side of ears yellowish-red; tail with dorsal black stripe and tipped with black; parietal ridges lyre-shaped, not forming a sagittal crest ..... *Urocyon cinereoargenteus*

30′. Upper parts yellowish-red; legs and feet blackish; outer side of ears blackish; tail without dorsal stripe and usually tipped with white; parietal ridges, if present, V-shaped, forming a saggital crest ..... *Vulpes fulva*

31.(29′) Total length less than 1350 mm; hind foot less than 200 mm; weight 20-45 pounds ..... *Canis latrans*

31′. Total length more than 1350 mm; hind foot more than 200 mm; weight 25-60 pounds ..... *Canis niger*

32.(28′) Tail more than 500 mm; weight more than 100 pounds; teeth 32; four cheek teeth on each side of upper jaw ..... *Felis concolor*

32′. Tail less than 200 mm; weight 15-25 pounds; teeth 30; three cheek teeth on each side of upper jaw ..... *Lynx rufus*

33.(16′) Ear longer than tail; four upper incisors; tail a cottony tuft 34

33′. Ear shorter than tail; two upper incisors; tail not a cottony tuft 36

34.(33) Length of hind foot more than 115 mm; ears more than 100 mm; tail black; interparietal absent or indistinct in adult ..... *Lepus californicus*

34′. Length of hind foot less than 115 mm; ears less than 100 mm; interparietal present and distinct in adult 35

35.(34′) Total length more than 460 mm; upper parts grayish-brown, heavily intermixed with black, sometimes giving a spotted effect ..... *Sylvilagus aquaticus*

35′. Total length less than 460 mm; upper parts deep ochraceous buff with rust reddish suffusion over back and sides; sides grayer than back ..... *Sylvilagus floridanus*

36.(33′) Size large, total length more than 750 mm 37

36′. Size smaller, total length less than 750 mm 38

37.(36) Tail broad, flattened dorso-ventrally, scaly, rounded at end; hind feet webbed, split claw on second toe of hind foot ..... *Castor canadensis*

37′. Tail long, round, nearly naked, scaly; hind feet webbed; mammae on back ..... *Myocastor coypus*

38.(36′) External fur-lined cheek pouches present; claws of forefeet greatly enlarged; tail much shorter than head and body; upper incisors grooved..... *Geomys bursarius*

38′. External fur-lined cheek pouches absent; claws of forefeet not greatly enlarged 39

39.(38′) Cheek teeth always more than three in each jaw; infra-orbital foramen never a long vertical slit; tail thickly haired or bushy..... 40

39′. Cheek teeth never more than three in each jaw; infra-orbital foramen a long vertical slit; tail not bushy 44

40.(39) Fore and hind limbs connected by a loose fold of skin; tail well furred, flattened horizontally, sides nearly parallel; pelage soft, dense and very fine; eyes very large ..... *Glaucomys volans*

40′. Fore and hind limbs not connected by a loose fold of skin; tail not flattened horizontally 41

41.(40′) Longitudinal light and dark stripes on back; tail moderately long, not very bushy ..... *Tamias striatus*

41′. No longitudinal stripes on back; tail bushy 42

42.(41′) Tail long, more than one-fourth of the total length; hind foot less than 75 mm 43

42′. Tail short, about one-fourth of the total length; hind foot 75 mm or more; body robust and heavy; incisors whitish on anterior faces..... *Marmota monax*

43.(42) Lateral hairs on tail tipped with white; grayish-white below; five cheek teeth on each side of upper jaw, first minute ..... *Sciurus carolinensis*

43′. Lateral hairs on tail not tipped with white; rufous below; four cheek teeth on each side of upper jaw ..... *Sciurus niger*

44.(39′) Upper molars with three longitudinal rows of cusps; tail usually scaly and sparsely haired, annulation very apparent and not concealed by hair..... 45

44′. Upper molars with two longitudinal rows of cusps or with numerous transverse enamel folds and triangles; tail usually not scaly and with annulations nearly or completely concealed by hair (if scaly, tail is thinly but distinctly haired) 47

45.(44) Size small; no color contrast between upper and lower surfaces of body; mixed yellowish-brown and black above, ashy-gray below; hind foot less than 22 mm; tail less than 100 mm; no heavy ridges on skull..... *Mus musculus*

45′. Size large; color of upper and lower surfaces of body contrasting; hind foot more than 22 mm; tail more than 100 mm; heavy ridges over orbit and posteriorly on skull 46

46.(45′) Body brown above and gray beneath; tail shorter than head and body; ears small, half buried in fur ..... *Rattus norvegicus*

46′. Body blackish above, yellowish-white below; tail longer than head and body; ears large, standing out from fur ..... *Rattus rattus*

47.(44′) Tail scaly and compressed laterally; hind feet partly webbed; size large, total length more than 500 mm ..... *Ondatra zibethicus*

47′. Tail rounded in cross section; feet not webbed; size small, total length less than 400 mm 48

48.(47′) Tail very short, usually less than one-fourth of the total length..... 49

48′. Tail relatively long, more than one-fourth of the total length..... 50

49.(48) Tail scarcely longer than, or shorter than, hind foot, brownish above, whitish below; nail of first (inner) digit of forefoot flat and strap-shaped; back dark brown, very heavily suffused with black; grizzled on head; underparts gray; upper incisors with a distinct groove near the outer edge..... *Synaptomys cooperi*

49′. Tail distinctly longer than hind foot, usually of same color as back, upper and lower surfaces not of contrasting color; nail of first digit of forefoot not flat and strap-shaped; back bright russet brown to brownish-chestnut; fur of underparts gray tipped with buff or cinnamon; upper incisors not grooved ..... *Microtus pinetorum*

50.(48′) Tail thinly haired, annulations not concealed by hair, giving scaly appearance; body size medium, rat-like appearance 51

50′. Tail usually well haired, annulations nearly or completely concealed by hair; body size medium to small 52

51.(50) Tail usually equal to or longer than head and body, may or may not be bi-colored; feet whitish; upperparts grayish-brown, somewhat grizzled; underparts whitish or grayish-white; fur soft, smooth to touch; temporal ridges forming pronounced bead on sides of skull above orbits..... *Oryzomys palustris*

51′. Tail usually shorter than head and body, blackish or dark gray on upper surface, grayish below; feet grayish; upper-parts grizzled buff and black; underparts grayish or buffy; fur coarse, rough to touch; cusps on cheek teeth flattened and divided into S-shaped lophs ..... *Sigmodon hispidus*

52.(50′) Total length more than 250 mm; tail more than 120 mm, well haired, distinctly bi-color; feet and underparts white or grayish-white; upperparts grayish-brown ..... *Neotoma floridana*

52′. Total length less than 250 mm; tail less than 120 mm 53

53.(52′) Underparts usually distinctly lighter than upperparts; back some shade of gray or brown; belly white or grayish-white; feet white; upper incisors not grooved on anterior face 54

53′. Underparts usually only slightly lighter than upperparts; back brownish or grayish; belly dusky or buffy; feet grayish or buffy; upper incisors grooved on anterior face 59

54.(53) Tail well haired and distinctly bi-color..... 55

54′. Tail usually thinly haired and not distinctly bi-color 57

55.(54) Tail with prominent tuft of hair at tip (pencilled), usually about equal to or longer than head and body ..... *Peromyscus boylii*

55′. Tail only slightly or not at all tufted at tip, about equal to or shorter than head and body 56

56.(55′) Size small; tail sharply bi-color and usually shorter than head and body ..... *Peromyscus maniculatus*

56′. Size medium to large; tail bi-color but not always with sharp division, usually equal to or slightly shorter than head and body ..... *Peromyscus gossypinus*

57.(54′) Hind foot usually 23-24 mm; ear about 18 mm from notch; fur long; blackish dorsal stripe on back; skull 30 mm or more in length ..... *Peromyscus gossypinus* (see 56′)

57′. Hind foot usually less than 23 mm; ear usually about 15-16 mm from notch; fur short; no blackish dorsal stripe on back 58

58.(57′) Ears same color as body, usually about 16 mm from notch; hind foot usually about 17-18 mm; color a rich tawny golden, inter-mixed with blackish hairs in some pelage phases ..... *Peromyscus nuttalli*

58′. Ears contrasting with body color, generally gray or blackish, usually less than 16 mm from notch; hind foot usually about 20-21 mm; color of upperparts pale to rich reddish-brown ..... *Peromyscus leucopus*

59.(53′) Light ochraceous-buffy above, orange-buff on sides; belly grayish-white, usually washed with buff; tail brown above, grayish white below, usually more than 70 mm ..... *Reithrodontomys fulvescens*

59′. Upperparts duller, grayish to ochraceous or brownish; belly grayish white; tail usually less than 70 mm 60

60.(59′) Upperparts brown mixed with cinnamon ..... *Reithrodontomys humulis*

60′. Upperparts brownish-buff with intermixture of blackish hairs ..... *Reithrodontomys megalotis*

61.(14′) Size large, more than four feet high at shoulders; tail straw-colored; upper row of cheek teeth more than 110 mm long; knob-like canine tooth at union of maxillary and premaxillary bones ..... *Cervus canadensis*

61′. Size smaller, less than four feet high at shoulders; tail brown above, white below; upper row of cheek teeth less than 110 mm long; no canine tooth present ..... *Odocoileus virginianus*

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Ecology of the Mountain Sheep

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Most of the field data herein presented were obtained by the writer as an employee of the Wyoming Fish and Game Commission while studying the decimating factors affecting the Rocky Mountain bighorn sheep (*Ovis canadensis*), in the Gros Ventre area of northwestern Wyoming. Prior to the initiation of the actual study, Dr. John W. Scott, Executive Secretary of the Wyoming Fish and Game Commission, gave the author permission to use such ecological data as herein contained. The field study extended from November, 1938 to October, 1939 during which bands of sheep were kept under almost daily observation.

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Classification and Distribution

The majority of mountain sheep belong to the genus *Ovis*. Two exceptions are the Asiatic blue sheep, *Pseudois*, and the maned sheep of North Africa, *Ammotragus*, both of which possess certain hercine characteristics that attest to the close relationship between the true goats and sheep.

Two species of mountain sheep are recognized for North America, the heavy-horned, *Ovis canadensis*, and the thinner-horned, smaller-bodied, more northern species, *O. dalli*.

The range of *Ovis canadensis* begins approximately 120 miles south of the Peace River in Canada and extends south into west Texas, northern Mexico, and the peninsula of Lower California. It consists of seven subspecies. *Ovis dalli* ranges from north of the Arctic Circle in Alaska south to the Peace River in the Canadian Rockies and including the Kenai Peninsula. It consists of three subspecies.

Paleontological evidence gives no indication that mountain sheep have ever occupied the mountains of eastern North America. In their present state, few if any of these mountains appear suited to mountain sheep. If, during earlier periods the mountains displayed the proper conditions, it is probable that the great central plains acted as a barrier to any possible eastern migrations. Nor have wild sheep ever been recorded from South America. However, a possible fossilized skeleton of a mountain sheep has been reported from Nicaragua (Cowan, 1940) which might indicate that the sheep once ranged considerably further south than they do at present.

The Old World possesses 11 recognized species of mountain sheep, with at least 32 subspecies. In addition to the Genus *Ovis*, this area of the world

claims two genera, mentioned earlier, not found in North America. Most of the Old World sheep are found in Asia; some are found on several of the Mediterranean Islands; and one species is confined to the mountains of North Africa. No mountain sheep are reported as living in any of the mountains of Europe although Duncan (1877) reports that wild sheep (probably *Ovis musimon*) were once found in Spain. Other types of mountain mammals such as the chamois and ibex are presently found in Europe. Possibly some type of antagonism between these species and the mountain sheep has discouraged the sheep from becoming established. In the Salmon River section of Idaho where both mountain sheep and Rocky Mountain goats live in adjacent areas it is said that the two species do not regularly mingle. According to Sheldon (1911) the range of the mountain goats in Alaska ends where that of the sheep begins. What discourages a potential intruder from taking over an ecological niche already occupied is an interesting problem. The ability of a species to defend itself against intrusion may not be the sole answer. It would hardly seem to apply in the case of the rather benign mountain sheep.

Mountain sheep the world over seem to confine themselves to areas north of 25°N latitude. Thus their distribution follows very closely Wallace's (1892) ecological delineations. In the New World, their distribution is remarkably congruous with his Neartic boundaries, and in the Old World their distribution follows very closely his Paleartic boundaries.

PHYSICAL CHARACTERISTICS

In external appearance the sheep are noteworthy for their relatively short legs, powerful shoulder development, and general stockiness, adaptations that are in keeping with their mountain-climbing abilities. The hoofs are also specialized for climbing in steep, rocky conditions. The posterior half of each digit bears a rubbery pad, which is a help in gripping smooth surfaces, and with the two digits of each hoof being independently moveable it is possible for the animal to cling to uneven surfaces. The front hoofs are larger than the hind hoofs and are apparently of greater importance in climbing and in facilitating difficult descents.

An obvious sexual dimorphism among mountain sheep is illustrated in the immense horns of the rams as compared with the relatively abbreviated counterparts among the ewes. The ewes also average only about one-half the weight of the rams, although in actual body measurements the two sexes are almost equal.

Interdigital glands characterize mountain sheep and they evidently secrete a rather persistent odor, for rams during the rutting season while traveling between bands of ewes are frequently seen sniffing the ground in a hound-like fashion. Suborbital glands which are also typically present are thought to produce the characteristic sheep-like odor, which is very evident around the bedding grounds but is otherwise not particularly strong among bighorns.

The fame of the mountain sheep for traversing narrow ledges and climbing almost vertical cliffs needs no embellishment. One is inclined, however, to overlook their nimble adroitness in maneuvering among broken terrain and their equal celerity in rapidly climbing or descending ordinary steep slopes.

These latter two qualities are important considerations, for much of the country in which sheep are seen can be more accurately described as being steep and broken rather than consisting of precipices in the usual sense.

Although by no means slow of foot, mountain sheep are not to be considered fleet animals. They seem to be capable of short bursts of speed, but sustained flight at high speed does not appear to be part of their makeup. They are said to be rather easily caught by dogs when cut off in open country away from their usual rugged surroundings, and Grinnell (1928) says they are readily overtaken on horseback in open country.

EVOLUTIONARY IMPLICATIONS

It is generally recognized that the mountain sheep originated in Asia (Cowan, 1940), probably in the Himalayan area, and from that focus they spread east and west through more or less continuous mountainous areas, crossing to other nearby land masses via land bridges, many of which have since disappeared. Thus, there is a general continuity in their distribution from northern Africa and some of the Mediterranean islands at one extremity, through the temperate and subarctic areas of Asia to North America, at the other extremity. More or less isolated populations living under differing environmental conditions tended to produce variations from the parent stock, forming the numerous species and subspecies of the past and present. Since the mountain sheep do not have a large ancestry of related species, it is probable that they are of relatively recent origin.

Among the Bovidae we find great variation in size and form, from the long-legged, fleet-footed antelope types to the various stocky, short-legged, slow-moving forms like the cattle, etc. One would suspect from the apparent, but somewhat clouded, relationship which is implied between the Cervoidea, Antilocapridae, and Bovoidea that the long-legged, fleet condition is the hereditary bovid type, since the Cervoidea, and perhaps the Antilocapridae, appear to be the older groups.

That such a fleet condition may have preceded the sheep is also indicated in the relationships existing between present-day mountain-dwelling bovids. The most primitive group of bovid, mountain-dwellers appears to be the goat-antelopes, tribe Rupicaprinae, and among this group, in turn, the most primitive member is the serow (Allen, 1940), which is a long-legged, fleet-footed animal, more reminiscent of the cervids or antelopes. Nevertheless, it lives exclusively in rugged, mountainous conditions and is said to have the climbing powers of the chamois (Kingsley, 1884). Other members of the tribe Rupicaprinae which tend toward a more sheep-like morphology are the more modern chamois and Rocky Mountain "goat."

The true goats seem to hold a position intermediate between the goat-antelopes and the mountain sheep. As possible integrades between the goats and sheep one finds the maned sheep and the blue sheep. These are classified as sheep, but have many goat-like characters, and extend the body-type series to that of the shorter, heavy-bodied, slower-moving mountain sheep of the genus *Ovis*.

From the foregoing, the implication would seem to be that the mountain sheep, which today are stocky, comparatively slow-moving, mountain-dwellers,

have evolved from distant precursors which were fleet animals of the cervid or antelope type and probably plains-dwellers. It may be that the evolutionary line culminating in the sheep included precursors to the sheep who were also mountain-inhibiting animals, and with development taking place in an environment where a quick dash into nearby crags always afforded complete protection, it has resulted in a deemphasis of fleetness and fighting ability, and an emphasis upon stockiness for mountain climbing.

ORIGIN OF NORTH AMERICAN SHEEP

All evidence points to the fact that the forebearers of our present North American mountain sheep arrived on this continent relatively recently; fossil remains are found no earlier than the Pleistocene. There appears to be no doubt that the original stock migrated to this continent from Asia, across the land bridge which has existed at various times between the two continents.

Cowan (1940) postulates that *Ovis nivicola* of eastern U.S.S.R., or a form common to both it and the North American *O. dalli*, is ancestral to all North American forms. It is his contention that as this ancestral stock moved southward in North America into new environments, various new forms gradually evolved. The rather sharp, present-day specific differences between *O. dalli* of the north, and the more southern *O. canadensis* is explained by Cowan on the basis of the glaciers which separated the North American sheep into two groups isolated above and below the ice sheets. By the time the ice had retreated, the two groups showed morphological differences great enough to justify classifying them as distinct species, *O. dalli* and *O. canadensis*.

There are several additional facts, however, which deserve attention in explaining the origin of the two North American species, and these lead to a second possible theory as to their origin. First, according to Nelson (1931), the time of first occupation of this continent by *Ovis dalli* appears to have been much more recent than the time of first occupation by *O. canadensis*. Second, according to Sushkin (1925), *O. canadensis* more closely resembles the sheep of inner Asia than it does *O. dalli* or *O. nivicola*. According to him, *O. canadensis* and the Asiatic argali, *O. ammon* are probably in direct genetic relationship. One might suspect this from outward appearances, and some early authors actually refer to *O. canadensis* as the American argali. On the other hand, *O. dalli* is recognizably similar to *O. nivicola* of eastern U.S.S.R., and the latter species is distinctly different from any other Asiatic species. The sharp morphological differences between *O. dalli* and *O. canadensis* might likewise cause one to question the lack of a direct relationship between the two. This is particularly true when the above-mentioned, close resemblances of the two North American species to two different Old World species is considered.

It is generally agreed, Snider (1932) that during the four different glacial advances which occurred during the past million years of the Pleistocene, land bridges were formed across Bering Straights between Asia and North America. The fourth and last land bridge probably existed as recently as twelve thousand years ago. Furthermore, it appears that habitable areas of Alaska including perhaps the Aleutian area existed during the ice periods where migrants could have maintained themselves. Thus the earlier *Ovis*

ammon type entered North America across one of the earlier bridges and moved southwards during the following interglacial period to be cut off by the next succeeding ice invasion. The *O. nivicola* type then entered North America across a later land bridge, perhaps even the most recent, and now, as *O. dalli,* is limited to regions continuous with the area of its first establishment on this continent.

RECENT HISTORY IN NORTH AMERICA

According to Seton (1929), mountain sheep in North America may have numbered as many as two million individuals prior to the appearance of white man. Early explorers sometimes recorded that in certain areas sheep were the most abundant animals present. The mountain sheep must have prospered during their early history on this continent, for they seem to have spread to all habitable niches within reach of their physical and psychological potentialities. All over the mountainous west, the frequent use of the words "bighorn", "ramshorn", and "sheep" in the naming of mountains, streams, and other geographical locations in areas where mountain sheep no longer occur, and the widespread occurrence of Indian pictographs portraying mountain sheep in areas where they are now absent, indicate that their former range included all habitable areas in the western mountain area of the United States, and some of the broken areas immediately to the east.

No doubt the sheep very early suffered from lack of conservation practices, but this seems insufficient to account for the rapid, almost cataclysmic, decline in mountain sheep numbers that occurred during the late 1800's and early 1900's. Observers on the scenes at the time invariably ascribed these terrific decimations to scabies contracted from domestic sheep (Seton, 1929). Almost without exception, these people made note of a correlation between losses among the wild sheep and the appearance of domestic sheep on the areas. Gradually the epidemics seemed to lose impetus, but not before the sheep had been reduced to a mere vestige of their former numbers, which is the condition that exists today.

THE GROS VENTRE SHEEP RANGE

GENERAL AREA

The herd of bighorn sheep herein referred to as the Gros Ventre herd, roam over a group of mountains and foothills that occupy an area of approximately five hundred square miles. The area consists largely of the Gros Ventre Mountains, which are located directly east of Jackson Hole, Wyoming. The country is drained by the Gros Ventre River drainage, and in part by the watershed of the Hoback River.

The Gros Ventre Mountains, which may be considered the hub and the major part of the sheep range, are not extensive. They are approximately forty miles long by fifteen to twenty miles wide. The highest peaks reach elevations of approximately eleven thousand feet. Timberline occurs at about 9,500 feet.

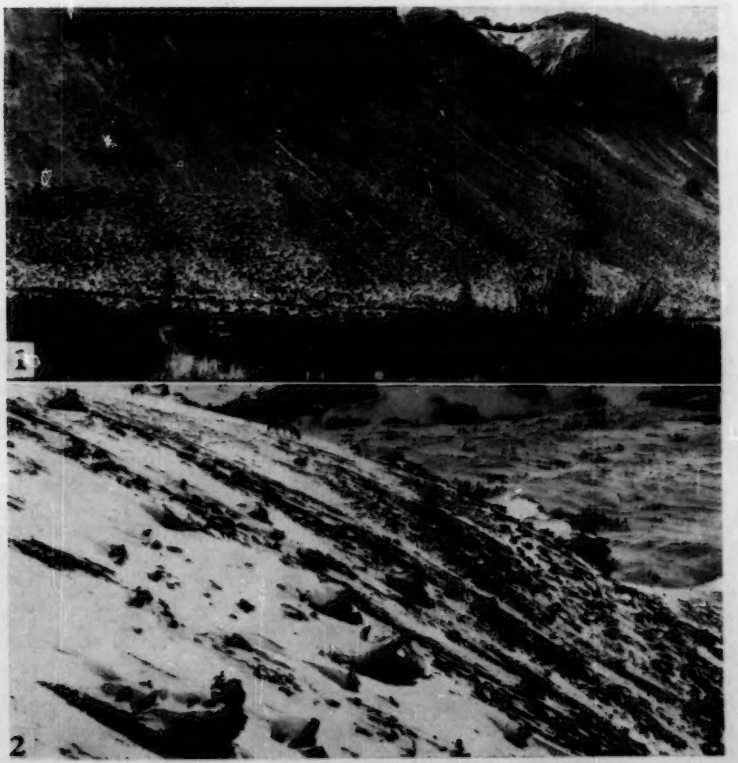
Most of the area is suitable for mountain sheep, but a sizable section in the western part of the area is heavily timbered, and is not used by the sheep.

Other sections, because they lack the necessary geographical characteristics, are likewise seldom if ever frequented.

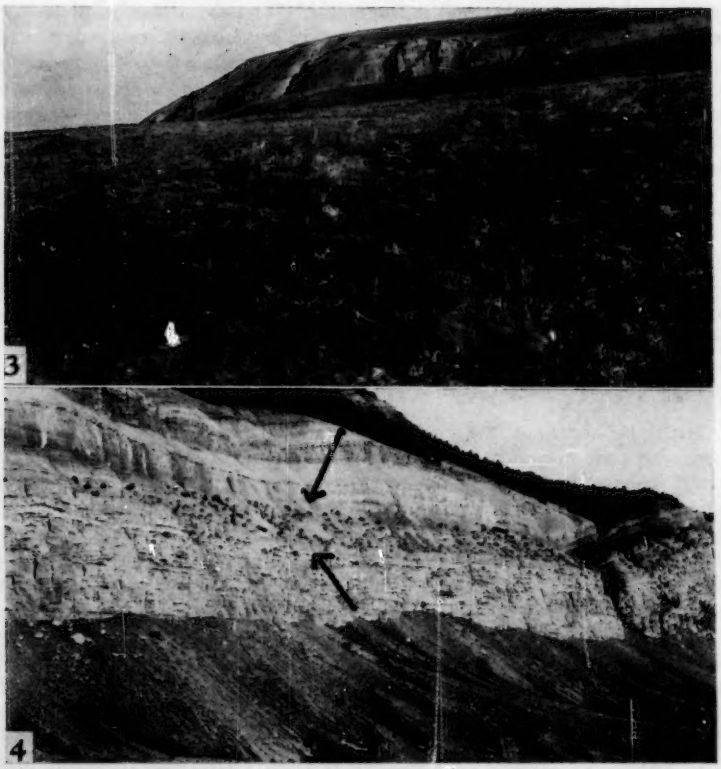
The characteristic feature of the Gros Ventre Mountains is their block-like character. As a rule, they possess broad, flat tops, which slope very slightly northeastward. These flat, mesa-like mountain-tops usually break off sharply into precipitous slopes. Many of the mountains are also cut by deep gorges and basins possessing steep, cliffy sides. The entire area is conspicuous for its broken, craggy conditions.

WINTER RANGES

The winter ranges of the Gros Ventre herd are located in six different areas, all at relatively low elevations. All have similar characteristics, consisting of a series of bluffs with south or west-facing slopes (figs. 1, 2). On such sites, the warm afternoon sun thaws the snow from the slopes soon after it



Figs. 1, 2.—1. The winter range in the Gros Ventre area consists of bluffs with south- or west-facing slopes, where the warm afternoon sun thaws the snow soon after it falls. 2. Wind-swept areas just above the cliffs are favorite feeding sites during the winter.



Figs. 3, 4.—3. The summer range on the Gros Ventre area consists of tundra-like plateaus located above timber line. 4. Inaccessible situations are resorted to shortly after the lambs are born. The area used in this instance, indicated by the arrows, was protected from above and below by sheer cliffs, and accessible in only one location.

falls, and the adjoining flats are swept free of snow by the predominantly westerly winds.

As soon as the thawing snows permit, the sheep begin moving toward the summer range, and they keep climbing progressively upward as the higher areas are released from their snowy covering. A series of cliffy ridges and rimrocked basins lead up from the winter ranges below, and in passing between the two ranges, the sheep assiduously travel by way of such ridges and interconnected crags.

SUMMER RANGE

High, plateau-like mountain tops, well above timberline, form the summer range. The sheep find an abundance of green forage on these tundra-like mesas, and the constant alpine winds keep their surroundings cool, and free of flies (fig. 3). Moisture is available in the form of snow, or springs fed by

melting snow. The steep, broken ledges which form the sides of all the mountains in this area provide an excellent, readily available source of protection. During the summer days, ewes, yearlings, immature rams, and lambs can be seen day after day feeding on the flat mountain tops, or on the steep slopes immediately beneath. The mature rams by this time have dispersed widely also into the high country and are found in the most inaccessible, craggy canyons and basins. Here, they roam singly, or in small groups. The two sexes appear to make a positive effort to remain separated during the summer and early fall.

A few ewes in the Gros Ventre area may remain in the lower, winter range the year around. Smith (1951) says that in Idaho a considerable number of sheep, including ewes, lambs, and immature rams, remain at the lower wintering altitudes during the summer. He suspects that the summer occupancy of winter ranges may possibly be correlated with the greater availability of salt at the lower altitudes.

LAMBING GROUNDS

Lambing occurs on the Gros Ventre area about the time the sheep are beginning their migration back to the summer range. Those ewes which are about to have their lambs tarry on the winter ranges; those in which parturition is not imminent, begin the shift to the summer range. Soon after giving birth to their lambs, the ewes are observed, often in small groups, in the most inaccessible conditions, where they remain for some days (fig. 4). One such area in this study was particularly noteworthy because the sheep were never seen there at any other time. It consisted of a very steep, almost barren slope, several hundred yards long, and protected from above and below by perpendicular walls. In only one place was it possible to make a descent, although a hazardous one, to their hideout. The ewes appeared to have resorted to this location shortly after giving birth to their young.

BEHAVIOR OBSERVATIONS

WARINESS

If undisturbed, the mountain sheep tend by nature to be unsuspicious animals. During this study, the ewes and young animals proved to be the most tolerant of human presence, some bands occasionally allowing themselves to be photographed. The mature rams, however, probably as a result of hunting pressures, were extremely apprehensive and would usually take flight at the sight of anyone. The sheep seem to depend upon an amazing visual acuity and a sensitivity to unusual sounds to makeup for a somewhat obtuse sense of smell.

In the early days, mountain sheep were reported to be simple, gentle, unsuspicious animals, and more easily killed, for this reason, than any of the other big game animals. In the primitive wilderness of the upper Yukon, Sheldon (1911) found that even after several members of a band had been shot, the rest of the sheep might stop and look at him, occasionally delaying long enough to afford an opportunity for a photograph.

REACTION TO DANGER

The fact that the mountain sheep tend to be somewhat trusting when

they are not disturbed does not mean that they are oblivious to danger. On the contrary, they are usually nervously alert and constantly on guard against proven enemies, and their phenomenal eyesight is a great asset in this regard. Bands of sheep under observation will on occasion suddenly become startled, often for no discernible reason. Then again, the source of fright can be perceived, sometimes at a great distance. Should an enemy show itself, even a long way off, the entire band with remarkable unity will make a headlong dash for the nearest rimrocks. There never seems to be any confusion on the approach of danger; their flight is always immediate and direct. The nearest cliffy ledges are always the objective.

MATING HABITS

The mountain sheep, as evidenced in this study, are completely polygamous. The rams do not attach themselves to any particular band of ewes; rather they are constantly on the move, traveling from one band of ewes to another. So frantic is the pace that the rams hardly stop long enough to feed. This continues for about a month (December).

When the rams first approach a band of ewes they begin to search out any individuals that are in oestrus. If none is found, they may lie down for a short time, stop to graze a bit, or continue directly on to another band. When a ewe in oestrus is found, she usually takes off on the run, and a remarkable chase over the most rugged terrain ensues (field notes, Dec. 8, 13, 17, 21, 1938). On casual observation the ewe appears to be trying to escape, but closer study rules this out. When the ram seems to be tiring or becomes discouraged, the ewe will sometimes stop until the ram catches up; then she will dash ahead once more (field notes, Dec. 8, 17, 1938). On the otherhand when the ewe becomes tired she will sometimes lie down, while the ram stands beside her, after which the chase begins again. If the ram closes in on the ewe, she will sometimes dodge and feint with the greatest skill, and then take off on the run once again (field notes, Dec. 10, 1938). Such procedure may have a selective effect, tending to favor the strongest and most agile. As many as four rams were seen in pursuit of a single ewe (field notes, Dec. 10, 1938).

For the most part the rams ignore one another during the breeding season, although despite this surprising lack of antagonism, butting jousts occur from time to time, sometimes with great ferocity. These contests, on the surface, appear to be somewhat pointless, for the participants seem to part on amicable terms once the joust is over.

During the height of the rutting season, three old rams were repeatedly observed off by themselves away from the other sheep. These individuals never seemed to enter into the rutting activity (field notes, Jan. 1, 1939). There are also reports of old "bachelor rams" who remain in the higher country all winter, never coming down to associate with the ewes on the winter range.

It is likely that only the strongest of rams are able to withstand the general physical strain of the entire mating procedure—the chases, the butting jousts, and the frenzied traveling between bands. Quite possibly it also limits the number of breedings by any single ram.

CARE OF YOUNG

In some respects, care of the young is solicitous, but there are definite evidences, also, of a certain carelessness. In favor of the ewes in this regard is the fact that they usually resort to inaccessible locations soon after the lambs are born and remain close to their young for about a week. During this period they apparently cache the lambs while they do their feeding.

The question of whether mountain sheep cache their lambs has been somewhat controversial. Spencer (1943) denies it, however, a number of experiences during this study indicated that they possess this ability. One experience clearly demonstrated such a control by the ewe. On this occasion (field notes, June 16, 1939) I was guided by the repeated sorties of a feeding raven to a freshly cast "afterbirth", which from the tracks present was manifestly that of a ewe. It was apparent that birth could not have been more than a few hours earlier, since a previous shower of rain would have at least partially obliterated the tracks. After a short search, a ewe was startled from among a group of boulders, and as she dashed off, the little lamb arose and ran after her. In her hurried attempt to escape, the ewe was noted to look back over her shoulder at her offspring attempting to keep pace, and as if realizing that this was impossible, she suddenly stopped, whirled around, and emitted the nasal snort, a sort of "chu," characteristic of mountain sheep. With it, the lamb immediately dropped to the ground. Then, without further hesitation, the ewe continued her flight. The signal apparently served to hold the lamb completely immobile, for it was possible to approach it and even fondle it without the slightest reaction, although its heart could be felt beating strongly beneath its still moist pelage. From time to time the mother would appear, scanning nervously from behind some protecting boulder, and several times she repeated the same vocal "chu". I withdrew, then, and returned after several hours, but the ewe and her lamb had left the scene.

There also is evidence that a single ewe will sometimes care for a number of lambs while their mothers thus freed are off feeding by themselves.

An adverse characteristic of the mountain sheep is that lambs, when still very young, perhaps within a week after they are born, begin following their mothers. The danger is that when enemies appear, the ewes frequently dash for safety, leaving the lambs to follow along as best they can. Then too, the lambs are sometimes reluctant to follow their mothers during pressing situations (field notes, June 15, Sept. 8, 1939). A somewhat unrealistic attitude pertains, therefore, as far as the protective relationship between mother and offspring is concerned, part of which appears to be the result of a certain stupidity on the part of the lambs themselves. As a consequence a susceptibility to predation on the part of the lambs is indicated.

FIGHTING ABILITY

Despite indications of some defensive abilities on the part of the rams, observations in this study indicated that the mountain sheep, on the whole, depend upon quick flight into cliffy areas for protection, rather than upon any ability to fight off enemy attacks. Basically, they do not seem to be fighters.

Various oral reports indicate that the rams will stage a fight if attacked

where flight is impossible. A very reliable resident of the Gros Ventre reported that he witnessed a ram successfully defend itself from a group of five coyotes (field notes, Jan. 16, 1939). The ram, he says, ran to a mass of rocks where by turning its back on the coyotes and using its hind hoofs, it was able to beat off the attackers. Frequently during this study it was observed that the rams travelled with greater impunity away from their cliffy protections than did the ewes. Twice on Feb. 20, 1939 (field notes) I saw coyotes pass within twenty-five yards of rams without any noticeable concern on the part of the sheep. A similar indifference would never have been the case had these been ewes. Murie (1944) in Alaska indicates that rams, in a group, display defensive tactics. When approached by wolves, they gather in a close circle with their heads and impressive horns turned toward the outer perimeter.

Cronemiller (1947), in describing the remains of a bighorn sheep which had been killed by a mountain lion, says the evidence indicated a considerable struggle on the part of the sheep before succumbing. Whether the struggle resulted only from an attempt on the part of the sheep to escape, or whether it actually fought the lion is not indicated. Possibly it was not discernible. McAdoo, as quoted by Davis and Taylor (1939), witnessed a bighorn ewe successfully defend its lamb against the attack of a golden eagle.

As an indication of lack of combativeness, however, game wardens who live-trapped bighorns in the Gros Ventre area earlier, said that the largest of the animals could be handled with no sign of fight. Hornaday (1914) says that mountain sheep, when brought to bay by dogs, become panic-stricken, and if cornered on a narrow ledge, they will leap to their death rather than fight.

REACTION TO CLIMATIC CONDITIONS

Mountain sheep as a group seem to be able to withstand almost any degree of low temperature, as attested by the fact that they are found above the Arctic Circle. Farther south, they seem to prefer the coolest possible conditions in any local area. However, they apparently have been able to adapt themselves, at least to a limited extent, to warm conditions, because mountain sheep are known to occur in some of the hottest desert areas of North America where summer temperatures commonly rise well above 100 degrees. Nevertheless, it appears that mountain sheep are exclusively animals of the temperate to cold climates, for where potential paths of migration lead toward tropical, and possibly more ideal conditions, they invariably stop far short of reaching those areas.

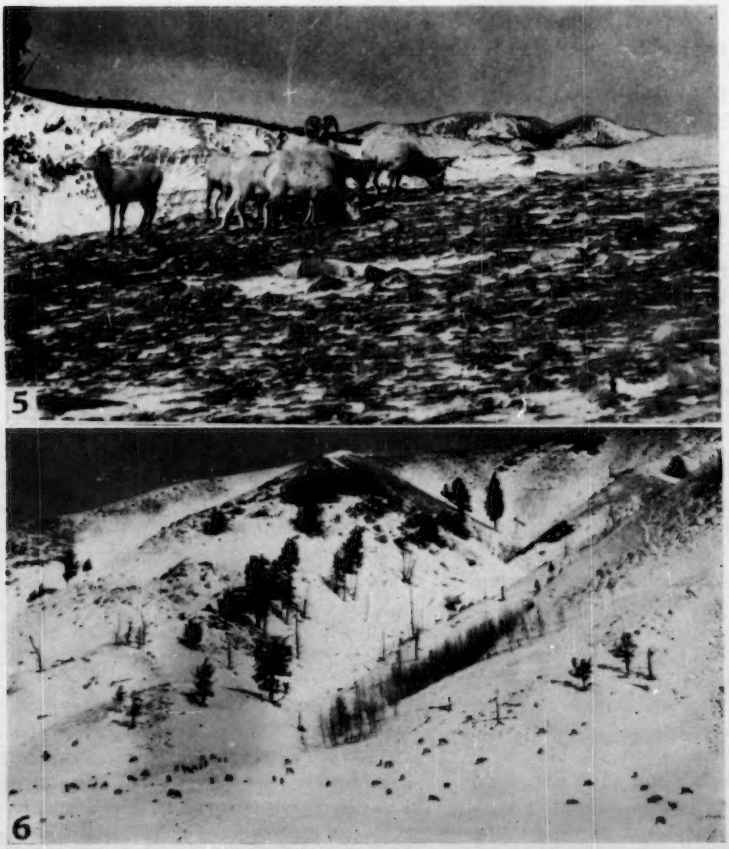
Despite their preference for colder climates, the mountain sheep from evidence in this study do not like snowy conditions. It was observed (field notes, Nov. 26, Dec. 9, 1938; Jan. 25, 1939) that their strayings from the ridges and cliffs were conditioned on the basis of the depth of snow on the surrounding areas. Following the thaws of warm weather, they would tend to forage more widely. Sometimes in traveling between cliffy areas they were required to traverse snow-covered conditions and while it did not seem to hinder them greatly, they displayed an obvious uneasiness while doing so (field notes, Jan. 13, 1939).

Cowan (1940) states that mountain sheep are noticeably absent from the western slopes of the Sierras, and also to some extent from the western

slopes of the Rocky Mountains. Rainfall is the heaviest on the west slope of both ranges and deep, persistent snow, along with thick forest growth, are characteristic of these areas. It is probable that these latter two factors are primarily responsible for the scarcity of mountain sheep on such western slopes, since neither deep, persistent snow, nor heavy forest growth favors the success of mountain sheep.

FEEDING HABITS

During the winter, the sheep do all their feeding among the cliffs; on the



Figs. 5, 6.—5. During the winter the sheep feed on restricted areas for prolonged periods, until the available forage becomes very closely cropped. 6. Early in the winter the elk like to graze in the valley bottoms and on open hillsides (foreground), but as the snow becomes deeper they begin feeding on wind-swept ridges and places where the sun thaws the snow (upper background). Here they compete directly with the mountain sheep.

slopes immediately below the cliffs; or on the flat areas just above the cliffs. Rarely do they stray more than a hundred yards from some kind of cliffy protection, although the rams are a little more venturesome. Wind-swept flats just above the cliffs, and slopes which are favorably situated in regard to the thawing rays of the sun are, therefore, their favorite winter feeding sites. They are able to uncover forage by pawing through snow, but their innate aversion to snow leads them to seek forage where it is already exposed, even though such forage has already been heavily cropped.

Winter habitats which meet the needs of the mountain sheep are limited in number and in area on the Gros Ventre range. For this reason, the sheep tend to forage on restricted areas for prolonged periods (fig. 5). As early as Dec. 10 (field notes) one such site had been cropped to within one-half inch of the ground. Still the sheep appeared to be finding enough nutriment to make feeding worthwhile. And, an area not more than six acres in extent was supporting a band of sheep as late as Feb. 21, 1939, having been a source of forage since the previous fall.

In the summertime there is an abundance of forage everywhere, but on the Gros Ventre range the sheep prefer to do their feeding on high plateaus above timberline.

FEAR OF TIMBERED AREAS AND OPEN EXPANSES

Mountain sheep seem to possess an inborn fear of extensive, heavily timbered conditions. The larger, forested tracts in the Gros Ventre district were entirely excluded from the usable territory of the sheep. However, the cliffy sections which they regularly occupied were interspersed with small wooded patches, and the sheep would occasionally enter them. As warm weather came on they were seen more frequently in sparsely wooded conditions, possibly for the cool shade afforded. In traveling between winter and summer ranges the mountain sheep avoided forested areas as much as possible, following the open ridges and crags.

Allen (1940) refers to a dwarf variety of blue sheep in Asia in which the animals had become separated from the rest of the normal, parent variety by a zone of thick, scrubby forest. The forested belt was no more than three or four miles broad; and yet, it appeared to present an absolute barrier. Down through the years, with the lack of intermixture between the two groups, it resulted in the development of a dwarf variety among the somewhat closely-confined group that had been isolated.

Broad expanses of unbroken, open country likewise hold a fear for the mountain sheep. They appear to completely refrain from entering upon any open stretches in which cliffy conditions are not at least distantly visible. In the Gros Ventre area they displayed an obvious dread of traversing any open area in which craggy conditions could not be reached by a short, quick dash.

On a number of occasions during this study, sheep were observed making narrow crossings between cliffy areas, and their behavior on such occasions aptly illustrated the fact that they consider such open conditions highly dangerous. They move as if feeling their way, advancing only short distances at a time, and interspersing each advancement with long, nervous pauses. They

cling to the broken conditions until it becomes absolutely necessary to break away (field notes, Jan. 13, 1939).

ORGANIZATION OF THE HERD

The social organization of the bighorn sheep seems to be largely that of a matriarchy. Bands of ewes are the stable core of the herd organization. Under the guidance of the ewes, and usually under the leadership of an old, experienced individual, the small groups of ewes and juvenile animals, move back and forth between summer and winter ranges.

The Gros Ventre herd, during both summer and winter, was split into various small bands. In some cases these were separated by considerable distances, as much as ten to twelve miles. Where the distances between bands was not great, there tended to be some inter-band migrations; otherwise they tended to remain intact. The number of individuals to be observed in any one band, however usually varied day by day. This variation resulted from the tendency of small sub-groups to split off on feeding excursions of their own.

In many respects, the ewes can be considered an entirely independent group of animals from the rams. It is only during the rutting season, from late November to about the middle of January that the rams and ewes intermingle regularly. A few rams sometimes prolong their association with the ewes beyond the rutting period, but by the time the migration back toward the summer range has begun, the two groups have completely separated. There are references in the literature (Allen, 1940) which indicate that in certain Old World species of mountain sheep, the bands are permanently led by old rams, who protect the band from enemies and the encroachment of other rams. This is in no way the case with the North American species. There is nothing in the way of a protective guardianship by the rams, not even in the form of a temporary, harem-like protectorship. Their function in the social scheme is entirely reproductive.

The rams have their own social organization, which, however, seems to be less distinct than that of the ewes. After the rutting season, they begin assembling into small bands composed of two or three to as many as ten or twelve individuals. During the summer, they remain entirely separated from the ewes by occupying different areas of the high summer range.

HERD MOVEMENTS

MIGRATIONS

Seasonal migrations seem to occur among most groups of mountain sheep. In the dry areas of southwestern North America, the animals are forced to change locations often, as a result of the vagaries of water availability. On the Gros Ventre mountain sheep range the urge to reach lower elevations during the winter seems to be dictated by a desire to reach areas relatively free of snow, rather than to any desire, in itself, for leaving the higher, colder elevations. In other districts, equally as far north, sheep are said to remain in high elevations all winter, or even to rise to higher elevations where favorable feeding conditions occur (Mills, 1937). Two winter trips were made during this study to the high country above timber line, but with the exception

of a single ram no mountain sheep were located. All had apparently migrated down to the lower ranges.

EMIGRATIONS

The evidence indicates that all suitable habitats were well stocked with mountain sheep during the early days, even non-contiguous mountain areas. It suggests that the sheep must have been prone to emigrate into new areas. Such movements probably occurred under conditions of population pressure, when the animals in local areas became overabundant. It appears that they may migrate to any suitable conditions within range of their eyesight, if the urge is great enough. This might constitute a considerable distance, because their vision seems to be as strong, if not superior to that of mankind. Davis and Taylor (1939) state that the bighorns in Texas commonly migrate seasonly as far as six miles between mountain ranges. Some of the emigrations of mountain sheep during the centuries past were no doubt farther.

FOOD HABITS

FORAGE

The mountain sheep are inclined to be delicate feeders, tending to nibble, and preferring the tenderest of plants. Basically they are grazers, showing a decided preference for grasses and forbs. However, when the occasion demands they are also capable of browsing on shrubby vegetation. It was obvious during this study that the sheep preferred green, grassy vegetation when obtainable. As the verdant, lawn-like covering of the mesa tops began to dry out, the sheep began restricting their feedings to those areas which were still green (field notes, Aug. 1, 1939). Then, as the entire mesa tops became browned, they began feeding on the slopes below, where springs kept small areas persistently green (field notes, Sept. 4, 1939).

It is rather doubtful that the particular type of forage available in any area has any delimiting effect on the distribution of the mountain sheep. Their ability to utilize such a wide variety of plant foods would seem to indicate an ability to get along in any suitable place where a sufficient quantity of food is available. The forage, however, must be procurable within their cruising radius, which is definitely limited.

Under starvation conditions, when the sheep are forced to browse for prolonged periods on woody plants such as willows, sharp splinters are likely to cause lesions in the mouth. Such open sores constitute foci for the establishment of the infectious disease, necrotic stomatitus.

MINERALS

Mineral licks were common in certain parts of the Gros Ventre area. Invariably they consisted of slit-like trenches which had been undercut by the licking or pawing action of the sheep. Sometimes the trenches were five or six inches deep and several yards long. All of the discovered licks were located on the winter ranges. The greatest activity around them seemed to be in the spring. In fact there were no indications that they were used at all during the rest of the year; there were no known migrations down to them during the summer.

Honess and Frost (1942) in Wyoming, record phosphorous pentoxide as being present in each of five licks analyzed. Sodium was found in only two samples, above trace amounts, and of these, chlorine was present in but one. Calcium oxide was present in three of the five samples. Packard (1946), in Colorado, reports that blocks of mineralyzed salt containing sodium chloride, phosphorous, calcium, and crude protein were made available to mountain sheep, along with blocks of plain salt (sodium chloride). He states that a band of twenty sheep consumed fifty pounds the first year, most of which was the pure sodium chloride.

It would appear that a source of mineral matter is a necessary constituent of mountain sheep habitat. Whereas the animals exhibit a decided appetite for sodium chloride when available, it is difficult to judge how much of this is eaten for "condiment" purposes, and how much is actually required for dietary needs. Calcium and phosphorous in mineral form are no doubt required as supplements to their natural diet, particularly in the case of ewes bearing young.

WATER

On no occasion were the mountain sheep of the Gros Ventre area observed traveling down to any of the many streams for purposes of obtaining drinking water. Nor were they ever observed drinking from any of the various temporary pools or streamlets, although more than likely they did so. The indications were that they preferred to eat snow for moisture. Snow was almost always available somewhere in their vicinity, even for much of the summer. Seton (1929) likewise indicates that mountain sheep actually prefer to obtain moisture by eating snow. In its absence, however, he says that they make daily, evening trips to sources of drinking water.

The evidence is that mountain sheep can go for long periods without water, possibly obtaining much of their required moisture from succulent vegetation. Hornaday (1908) as quoted by Smith (1951) says that the mountain sheep in the vicinity of Sonora, Mexico visited water holes so seldom that the Indians in the area called them "the animals which never drink."

It appears, in general, that availability of water has little to do with the pattern of success of mountain sheep. On a local level, however, it is quite likely that seasonal migrations are often governed by relative abundance of water, particularly in arid conditions.

NATURAL ENEMIES

The list of animals reported to be predatory on the mountain sheep includes the bobcat and lynx, *Lynx* sp., coyote, *Canis latrans,* mountain lion, *Felis concolor,* wolf, *Canis lupus,* and golden eagle, *Aquila chrysaitos.* Sheldon (1911) also lists the wolverine, *Gulo luscus,* and possibly the fox, *Vulpes* sp. Of these, only the coyote and eagle were abundant enough on the Gros Ventre area to be of importance. Bobcats, wolves, and mountain lions were known to the area, but they were not abundant enough at the time of this study to be significant.

The fact that mountain sheep cling so fanatically to their craggy protections and the fact that they are so nervously alert whenever they find it neces-

sary to venture away from the cliffs, would seem to be empirical evidence that predation might be an important factor.

Bobcats and lynxes

Bobcats were present on the Gros Ventre area at the time of this study, but they were not abundant enough to be considered important. According to Seton (1929), on two different occasions lynxes have been observed killing adult ewes by springing on their backs and fixing their teeth in the sheep's eyes. The two predators referred to were able to accomplish this feat despite the fact that they weighed only eighteen and twenty-two pounds respectively. Sheldon (1911) states that a lynx will sometimes watch mountain sheep for hours, and after sneaking to a point toward which they are moving, it crouches upon a rock and, as the sheep pass, it attempts to leap upon the back of one of them.

Coyotes

Coyotes were abundant in the Gros Ventre area, and many observations were made regarding their relationship with the bighorn sheep. All evidence indicated an unfavorable one. It became evident very early in the study that the sheep were more fearful of coyotes than they were of human beings. Any time a coyote appeared within sight of the sheep, they would immediately bolt for the nearest ledges, never hesitating long enough to determine whether an attack was forthcoming or not. On numerous occasions, bands of sheep under observation would suddenly make a break for the nearest cliffs, ostensibly unprovoked. Almost always in such instances, however, a coyote or coyotes could be spotted somewhere lurking in the distance to account for the sudden departures. There was no possible doubt that the sheep in the Gros Ventre area were living in constant fear of coyotes. The rams seemed to be considerably less concerned than the ewes, however.

To actually observe a predatory killing is not easily accomplished. In the first place, an area like the Gros Ventre district is so extensive and so rough, that only a small portion can be under observation at any one time. Second, attacks which are successful can hardly be frequent occurrences. Sheldon (1911) says that attacks fail far oftener than they succeed. This must necessarily be so, for at the rate of but one successful attack a day for the entire Gros Ventre area, and the entire herd, adults and all, would have been eliminated in approximately six months. Third, the presence of an observer on the area probably has some repressive effect on predator activity.

Nevertheless, two predatory attempts by coyotes were actually observed. One was an attack observed in the winter upon a mature ewe. The coyote was seen making a sudden dash after the ewe, who had been feeding on a steep, talus slope beneath a series of rimrocks. Although he came within approximately ten feet of catching her, she seemed to evidence very little trouble eluding him once she started ascending the slope. The coyote appeared to have made his rush from a higher point, and probably from behind some sort of concealment, there being a number of boulders and considerable bushy vegetation nearby.

Then, during the summertime, on the high summer range, a coyote was observed making a clever stalk of a group of sheep. A small group of three

ewes were being observed from a concealed location with my field glasses. They were feeding along the edge of one of the broad, flat mountain tops, when suddenly a coyote was seen, near the opposite side of the mesa, slinking toward the sheep. A few scrubby shrubs and an occasional rock outcropping were the only cover available on the otherwise smooth mountain top. However, he took advantage of these with utmost cunning, following a somewhat circuitous path so that some sort of cover continually screened him from the feeding sheep. He constantly maintained a low crouch, and moved with remarkable swiftness. Finally, he drew up behind a rock, perhaps fifty feet from the sheep, where he flattened himself against the ground to such a degree that he could not be seen, even with the aid of the binoculars. The distance covered was approximately 180 to 200 yards.

The ewes kept on feeding, but after about three or four minutes the ewe nearest the coyote suddenly threw up her head in an alarmed fashion, and ran about ten paces in the direction of the mesa edge. Thereupon, the other two ewes, alarmed, ran in the same direction. One continued to the very rim of the mesa, and in the next instant a lamb could be seen standing by her side; apparently it had been lying there. It is doubtful that the coyote, behind the rock, could have seen the lamb before it stood up, and possibly not even then, because a small ridge of earth intervened.

Evidently the first ewe to become alarmed had scented the coyote or had seen some suspicious movement. After her first sudden dash, she stood facing the rock behind which the coyote lay. Then, after a considerable pause, and as if prompted by curiosity, she look several steps in the direction of the rock; whereupon, the coyote stood up in full view. With that, the three ewes, with the lamb keeping pace, dashed down into the rimrocks forming the mountain side. The coyote, evidently realizing that the game was up, made no attempt to give chase.

There seemed no reason for suspecting that the coyote was stalking the ewes, since he had ample opportunity to attack them had he so desired. It seemed more probable that he was looking for lambs.

Many other coyotes were seen on this high, summer range. They seemed to be most abundant when the sheep first arrived on the mesas, but they were also seen from time to time all during the summer. On a number of occasions coyotes were startled from concealment under conditions which suggested their being a source of peril to the welfare of the mountain sheep. On the first such occasion a coyote was frightened from a lush growth of grass close to a small water hole, located well out near the center of a mesa. He was so well concealed, by simply flattening out against the ground, that I was within fifty feet before he became aware of my presence, my approach being from behind. Two days later, on a return visit, a group of five ewes and two lambs were seen feeding around the same water hole. In another instance, a coyote was frightened from a rocky ridge which overlooked one of the mesas. Directly out from the ridge a group of three ewes and two lambs had been feeding a few minutes beforehand, but had moved off.

On a third occasion a coyote was startled from his concealment along the edge of a mesa. Directly across along the opposite side of the mountain top

(about 200 yards distance) a group of five ewes and five lambs were observed feeding.

That the sheep had become aware of their danger was well illustrated by their behavior when moving out onto the mesas to feed. An old, lambless ewe would invariably be the first to emerge on top from the cliffs below. Very slowly, and with frequent, long pauses, she would venture out. Not until she was well out onto the feeding grounds would the other sheep follow, advancing slowly, and pausing whenever the lead ewe paused. The same procedure was observed as the sheep moved off the mesas. Then, too, the sheep seemed to evidence a positive effort to do their feeding in clear, open areas, away from rocks or scrubby growths, which were found in some sections of the mesas.

An attempt was made to keep track of ewes and their lambs, a somewhat difficult task, but a ewe which should have had a lamb could always be told by her swollen udders. The fact had to be recognized that when the lambs were very young they were sometimes tended in a group by a single ewe, while the other ewes, free of their lambs, were off feeding. Nevertheless, it was obvious that there was a lamb decrease soon after the ewes first began feeding on the high mesas. Ewes wandering about, bleating, in search of missing lambs were observed on a number of occasions during this period.

Coyote scats were collected whenever found, and they were analyzed by O. J. Murie of Jackson, Wyoming. Over two thousand were collected in various parts of the range. The returns from a representative sample of four hundred scats showed forty, or 10%, containing mountain sheep remains. In ten of these it was possible to identify remains from lambs, or from very young animals.

During the winter, also, a noticeable, gradual decrease in the number of lambs was indicated. Disease and malnutrition did not appear to be operative since no sick or undernourished individuals were seen, and the amount of forage, although not abundant, appeared to be sufficient throughout the winter. No clues in the way of carcass material were found, with the single exception of what appeared to be some lamb remains. This material was found in a ravine just beneath the bluffs of one of the winter ranges, and it consisted only of a matted mass of hair. All the bones had been consumed or dragged off.

COUGARS

Cougars were not a factor on the Gros Ventre area at the time of this study. None frequented the area, although they were present in the district earlier. Evidence elsewhere indicates that they will kill mountain sheep. Stone, as reported by Cronemiller (1947), found a recently killed bighorn sheep that, according to the tracks present, had been killed by a cougar. Packard (1946) states that in the Rocky Mountain National Park, three bighorns during the previous ten years had been reportedly killed by mountain lions, but without valid proof. Spencer (1943) says that one mountain lion was known to cover the Tarryal mountain sheep range of Colorado, and that during the year 1940, one bighorn killing was ascribed to predation by mountain lion.

Cahalane (1947) indicates that cougars may have an advantage over other four-footed predators when operating in the typical craggy habitat of the sheep. Smith (1951) states that a rancher and former state trapper in Idaho trailed a cougar to the freshly uncovered carcasses of six bighorn sheep, which had been previously cached.

EAGLES

The Gros Ventre area provided good opportunities to observe the relationship between the mountain sheep and the golden eagle. Eagles were constantly on hand during both the winter and summer seasons. In contrast with the constant apprehensive attitude of the sheep toward coyotes, the sheep seemed completely oblivious to the presence of eagles.

On one occasion, on the winter range and late in the spring just before the lambing season, an eagle behaved in an unusually suspicious manner. The bird flew in over a small band of mountain sheep and then hovered over them for a time. At one moment it was only about a yard above the head of a ewe. Despite the proximity of the eagle on this occasion, however, the sheep still showed no alarm. On several other occasions, eagles alighted in trees where they seemed to be engrossed in watching nearby bands of sheep. Such behavior was looked upon with suspicion, since eagles are not prone to spend much time in pointless perching, and the only times that I can recall their perching in trees was in the immedlate vicinity of the mountain sheep. However, although eagles were observed almost daily throughout the study, on no occasion did they ever make a strike at the mountain sheep, nor, for that matter did they seem to bother any of the other animals in the area. They appeared to be chiefly carrion feeders.

Despite the apparent amicable relationship between the eagles and sheep on the Gros Ventre area, evidence elsewhere indicates that they cannot be ignored as potential predators of mountain sheep, particularly of the lambs. Sheldon (1911) states that the eagle preys on mountain sheep lambs until they are six weeks or two months old. After that, neither sheep nor eagles pay any attention to each other. According to Grinnel (1928), the golden eagle has been seen killing animals as large as full grown coyotes and badger, and he says that wild sheep are also among those animals killed for food. Seton (1929) asserts that mountain sheep lambs when attacked by eagles are able to escape by crawling into bushes. Norris, as quoted by Mills (1937) states that golden eagles in Yellowstone National Park harass the mountain sheep and may cause the lambs to fall from the precipitous cliffs of their surroundings. McAdoo, as quoted by Davis and Taylor (1939) witnessed several attempts of a golden eagle to capture bighorn lambs and he states that the lambs were successfully defended by the mothers. Kennedy (1947) observed an eagle devouring a two-day-old lamb that was still warm, the indications being that the lamb had been struck down by the bird. Lark Green, of the Red Rock Ranch, told me that several years earlier he had seen an eagle near the Gros Ventre River flying with a lamb in its talons. While he watched, he related, the eagle dropped the lamb, and thus he was able to verify the fact that it actually was a mountain sheep lamb.

WOLVES

According to Murie (1944) wolves in Mount McKinley National Park, Alaska regularly hunt mountain sheep, hoping to find weakened individuals or to catch animals in vulnerable situations. Young (1944), from the same area, says that mountain sheep are a favorite food of wolves. However, Sheldon (1911) states that "the wolf is not very persistent in hunting sheep, preferring rather the caribou and the moose".

OTHER PREDATORS

Sheldon (1911) says that bears do not hunt mountain sheep, although they will feed upon the dead carcasses of sheep. He describes an instance in which a small group of mountain sheep passed within twenty feet of a sleeping grizzly bear. At one moment, he relates, the bear raised his head and looked at the sheep, but evidently not being interested, he lowered his head and went back to sleep.

In regard to foxes, Sheldon (*Ibid.*) says:

> After observing foxes in sheep country for several years, and after numerous examinations of their stomachs and refuse about their dens, I have no evidence indicating that they attempt to prey upon sheep, old or young. During several months' observations where sheep were abundant and when the snow was on the ground, fox tracks never suggested that foxes hunt sheep. It may be possible that they sometimes take lambs.

Jones (1950) refers to a report by F.R. Oberhansley (on file at Sequoia and Kings Canyon National Park Headquarters) in which it is stated that ravens, *Corvus corvax*, in Yellowstone National Park area are likely to attack newborn lambs, and pick out their eyes. This was not observed on the Gros Ventre area, however, where ravens were abundant.

DISCUSSION

The psychology of the mountain sheep which constrains them to remain in broken, craggy conditions, although it would seem to be to their disadvantage at times, appears to be accountable in part on the basis of a constant, innate fear of predatory attack. One might be tempted to go so far as to account for their original occurrence among such rugged conditions on their inability to defend themselves. However, as indicated in the section on "Evolutionary Implications", there is good reason to believe that their original occurrence in such an environment may not have been for this reason. Among these cragged conditions they find a great deal of choice forage, which, because of their expert climbing ability, is exclusively theirs. Quite likely their evolutionary origin took place in this type of habitat from immediate precursors who themselves were mountain-dwellers, and they fill a very definite ecological niche.

Some susceptibility to predation among the older animals, particularly the ewes, can be accounted for on the basis of their lack of fleetness and absence of innate fighting instincts. However, their ability to negotiate almost inaccessible ledges along with their capacity for climbing ordinary steep slopes with greater alacrity than most animals, seem to hold predatory losses among adult animals to a minimum. In the case of the young, however, a different situation seems to pertain. Shortcomings in the protective relationship between

the young and their maternal guardians, plus a certain degree of stupidity on the part of the young themselves, render them highly susceptible to predation.

Scarcity of lambs and yearling seems to be almost a universal, and quite likely normal, condition among mountain sheep herds. Even in relatively untouched areas this seems to be the case (Sheldon, 1932). Susceptibility to predation on the part of the young appears to be the most important cause, and it may serve as a natural method of preventing overpopulations.

ACCIDENTS

The mountain sheep, living under conditions which are intrinsically hazardous, inevitably suffer accidental injuries. Limping animals were commonplace on the Gros Ventre area, and more severe injuries were occasionally seen. Most of the latter seemed to be among the ewes. One ewe appeared to have a broken leg; another had a permanently deformed front leg with a large swelling above the knee. A third ewe seemed unable to place any weight on one front leg, and the hoof appeared to be broken; in addition, a patch of fur about four inches square was absent from both shoulders. A fourth ewe evidenced a considerable amount of blood on the side of the face, and she also appeared to have a lesion on the throat.

Rams also occasionally suffer accidental injury, often, perhaps, the result of their fraternal battles. During this study, the bloody trail of a ram was discovered during the rutting season, and rather profuse bleeding was indicated. A few days later, another ram, or possibly the same one, was seen, with blood-encrusted flanks. Mills (1937) reports finding a dead ram in December (the rutting season) with a cedar branch penetrating its side. Apparently it had fallen against the sharp branch, or had been pushed against it with great force. He also reports the case of a ram dying of a skull fracture. Near the base of one horn there occurred a cleft six inches long, and as wide as three-eighths inches. The head-on collisions of jousting rams sometimes result in terrific impacts. The resounding claps could sometimes be heard for miles on the Gros Ventre area. A large ram in the Gros Ventre herd had completely lost one horn; not even a visible stub remained. One of the local game wardens said that a number of years earlier a hunter had blasted a horn from the head of a ram by a misdirected shot, this possibly being the same individual.

From time to time, the sheep apparently have unfortunate encounters with porcupines, *Erethizon dorsatum*. During this study, the remains of a ewe with numerous porcupine quills penetrating the face was discovered on the summer range. In all probability, the imbedded quills had been the cause of death.

Several years prior to this study, the broken body of a lamb was found on the Gros Ventre area at the base of some precipitous cliffs, from which it had apparently tumbled. Packard (1946) also reports finding a dead lamb at the base of a cliff. Eagles, as mentioned earlier, are said to frighten lambs into plunging over cliff sides, but quite possible they occasionally also accidentally fall.

Jones (1950) contends that mountain sheep are sometimes killed in snowslides, and he further states that rock slides may occasionally catch them.

Parasites and Disease

During the years 1935 and 1936 winter mortalities severely decimated the sheep of the Gros Ventre herd. According to observers on the scene at the time, the heavy losses of that period were correlated with an acute pneumonic condition. I was told that the affected animals, coughing incessantly, would frequently stagger about and fall to the ground exhausted.

Marsh (1938) reports mountain sheep similarly affected in Yellowstone National Park, Glacier National Park, and at Sun River, Montana. He states that the bronchial cough was universal among the sheep which were in poor physical condition. Occasionally, he says, it even appeared among animals apparently in good flesh. Range conditions were known to be extremely poor during this period, a result of overgrazing and continued drouth. Even as early in the year as November, in 1934, Childs, as reported by Marsh (1928) observed coughing sheep on a range which was obviously badly depleted. Thus, a coughing, pneumonic condition often followed by severe decimations, seems to be a direct result of an impoverished range.

Both Marsh (1938) and Potts (1937) say that pneumonia among mountain sheep is caused by the bacterium *Pasteurella,* the causative organism of hemorrhagic septicemia, with *Cornybacterium* as a secondary invader. Newson, as quoted by Potts (1937), thinks that the bacteria may be present in healthy animals. Anything that weakens their resistance, such as malnutrition, then causes the infection to become pathogenic.

A disease likewise definitely correlated with a poor range situation is necrotic stomatitus. According to Cahalane (1937), it is particularly serious in young animals. The infection enters the tissues through cuts and lesions in the mouth, the result of eating rough, coarse forage usually under starvation conditions. Animals which recover from the disease have deformed jaw bones, and invariably show a loss of teeth. Except in the southwestern part of the United States where mountain sheep characteristically feed on rather coarse forage, they will not regularly consume woody material except under severe conditions of food shortage.

The heavy losses among mountain sheep herds during the late 1800's, as mentioned before, are said to have been caused by sheep scab contracted from domestic sheep (Seton, 1929). Apparently it was the disease known as common scab. This is a skin malady caused by the parasitic scab mite, *Psoroptes communis ovis*. In domestic sheep this parasite is no longer a serious threat. Dipping is a quick and satisfactory treatment. However, among wild sheep the disease would prove to be a serious factor. According to Hall, Dikmans, and Wright (1923), the infected domestic sheep become very restless and spend considerable time biting and rubbing the infected areas. This results in areas of bare pelage and in the appearance of sores. Without treatment, many of the sheep die as a direct consequence of the debilitating effects of the mite infestations. If they do not succumb from this cause directly, they are so weakened that they are killed by other diseases.

Jones (1950) cites two instances in California where bighorn sheep were

so decimated by scabies that the few remaining animals were unable to survive after the epidemics had subsided. Thus the two herds were totally destroyed.

According to Marsh (1938), the mountain sheep are hosts for a species of lungworm, *Protostrongylus*, which is apparently specific to the wild sheep. A different species is said to infect the domestic sheep. Mills (1937) says that in the sheep of Yellowstone National Park, lungworms (as well as scabies) have caused reductions in the herd. At present, both appear to be incipient in the animals, and are potentially dangerous.

COMPETITION

Mountain sheep tend to suffer disproportionately in any competition from other grazing animals. Whereas most other herbivores are able to range widely in search of forage, the mountain sheep seem psychologically bound to their restricted niche, and are forced to find forage within very limited boundaries. Thus, forage removed by competing animals from these restricted areas is particularly significant to the sheep, particularly during the winter months.

The most important competitors with the mountain sheep in the Gros Ventre district were elk, *Cervus canadensis*, of which there were large numbers. Only slightly less important, was competition from mule deer, *Odocoileus hemionus;* deer, however, were less abundant than the elk. No domestic sheep were found on the area, but cattle were fairly numerous.

ELK

The elk usually ranged widely in their foraging activities when unhampered by deep snows. During the early winter when there was little snow they did much of their feeding in the valley bottoms and in open park areas among the timber. As the winter progressed, however, and the amount of snow in the valley bottoms became deeper, the elk shifted their feeding activities, and began to graze more and more on wind-swept ridges and flats, and places where the thawing rays of the sun tended to keep the vegetation snow-free. Unfortunately, however, many of these locations proved to be within the feeding territories of the sheep (fig. 6). For weeks, bands of elk were seen feeding side by side with the sheep, and in direct competition for the same forage. However, since the sheep are able to crop forage more closely than do the elk, the sheep were able to glean some nutriment after the elk had moved on to better grazing. Another ameliorating factor regarding competition from elk lies in the fact that these large, heavy animals do not readily negotiate the steeper, craggy conditions where forage, in small patches, is sometimes abundant.

Packard (1946) says that following the introduction of elk into the mountain sheep range in Colorado it soon became apparent that competition provided by the elk might soon crowd the mountain sheep off the range.

In Yellowstone National Park, Mills (1937) says that the winter range had been so depleted by the foraging of large bands of elk that the bighorns were forced to feed on very short forage all winter.

DEER

Mule deer began appearing in late December on the lower sections of

the Gros Ventre area. By February their numbers had increased until bands numbering thirty to forty individuals were seen. After their first arrival, the deer did most of their feeding at the bases of the bluffs, where tall growths of black sage, *Artemesia tridentata*, occurred. This plant is almost totally ignored by both the mountain sheep and the elk, but it is evidently palatable to the deer. As the winter advanced, however, the deer began to work up into the cliffy areas occupied by the mountain sheep. The deer were being harassed by coyotes, and more than likely it was to escape their ravages that they resorted to these rougher, broken conditions. Here they began to feed on the two rabbit brushes, *Chrysothamnus pumilus* and *C. frigidus;* white sage, *Artemisia frigida;* and winter fat, *Eurotia lanata;* all of which are important winter foods of the mountain sheep. The deer evidenced more alacrity than the elk in getting around among the craggy conditions, and their competition with the mountain sheep, once they resorted to these conditions, was direct and constant. And, although the deer seemed to prefer the coarser foods mentioned, they also partook, to a considerable extent, of grasses, the favorite forage of the mountain sheep.

CATTLE

Cattle grazed over most of the Gros Ventre area during the summer and early autumn, but it is rather doubtful that their competition had any direct bearing on the mountain sheep. Most of their grazing was done in the valley bottoms and on open hillsides, locations not used by the mountain sheep. Indirectly, competition by cattle might be of some importance to the sheep since some of the forage consumed by cattle would otherwise be available to wintering elk. The elk, in turn, are competitors with the mountain sheep when forage in the valley bottoms and lower slopes becomes depleted or unavailable. Irregardless of the amount of forage available to the elk in the valley bottoms and lower slopes, however, deep snows usually eventually force the elk onto some of the favored feeding sites of the mountain sheep.

DOMESTIC SHEEP

Fortunately for the bighorns, domestic sheep were not grazed in the Gros Ventre area. Elsewhere, where they are permitted to graze on areas occupied by mountain sheep, they are considered to be serious competitors. According to Davis and Taylor (1939), both domestic sheep and domestic goats compete directly with mountain sheep where these species occur on the same range with mountain sheep. Thus, competition for food plus the fact that diseases are so readily transferred from domestic to wild stock render areas grazed by domestic sheep untenable for mountain sheep.

DISCUSSION

The mountain sheep are extremely efficient foragers and are capable of eking out an existence on feed that is very sparse. It is doubtful, therefore, that they very often succumb to actual starvation in the sense that food is totally lacking. However, when their range conditions become depleted to a point where only second-class foods are available, they tend to contract one of two fatal diseases, pneumonia or necrotic stomatitus. Thus, competition

from other grazing species can be a serious factor in the welfare of the sheep, even though starvation as such may not occur.

Permanent damage to vegetative growth can occur as a result of the intense feeding of wintering mountain sheep. On the Gros Ventre area the wintering sheep grazed for weeks on areas that had been cropped within less than an inch of the ground. In cropping so closely they inevitably uprooted occasional plants, but not frequently enough to be considered seriously destructive. However, in many places on the winter range the vegetative covering was very sparse or non-existent, suggesting that in previous years when larger populations are known to have roamed the area, intense grazing to the point of range destruction may have been the case.

THE ECOLOGICAL NICHE

TOPOGRAPHIC CONDITIONS

Almost any account of mountain sheep any place in the world will make reference to the broken, craggy habitat of the animals. This appears to be a universal characteristic of mountain sheep country, and a basic requirement of the animals. In the early days, according to Grinnell (1928), mountain sheep would sometimes range out onto the open prairies in the eastern part of their North American range. Buttes and rough, rocky conditions, however, were never more than a mile or two away. The animals, therefore, could in no way be considered prairie dwellers.

Large numbers of Audubon bighorns formerly existed in areas which are largely non-mountainous. These included the badlands of North and South Dakota, and the rough, broken terrain along the Yellowstone, Little Missouri and Platte Rivers. These localities, however, are characterized by craggy conditions, even though they are non-mountainous.

This then, would seem to be the number-one requirement of mountain sheep habitat; namely, broken, craggy conditions, irrespective of any altitudinal relationship. Thus, mountain ranges without such conditions (even though located proximal to occupied sheep country) do not support mountain sheep populations. And, non-mountainous areas, if they possess these necessary topographic features are potential mountain sheep environment.

CLIMATE

On the west-facing slopes of the western mountains of North America many areas exist which are ostensibly good mountain sheep country, but which do not support mountain sheep populations. It will be found, however, that heavy, persistent snows make food unavailable during much of the winter, and thus these areas are rendered untenable. Sometimes, on the east and south slopes of these mountains (normally the choicest locations), isolated patches of seemingly good mountain sheep country occur, which, however, have never supported sheep populations. A study of such areas will reveal them to be covered with deep snow during the winter, or to be too far removed from the proper topographic conditions which are snow-free. The animals will travel considerable distance to suitable winter range, but the routes to such ranges must be characterized by a relatively continuous series of cliffs and steep ridges. They cannot be depended upon to travel over

vast open areas, nor through continuous, heavy stands of timber to reach suitable range.

The sheep obviously prefer cool conditions. Where alpine areas are available, they make annual summer migrations to such conditions, in part, it would appear, to take advantage of the cooler temperatures. However, since the sheep exist where alpine conditions are not available, this seems not to be an absolute requirement.

FOOD

It is necessary that forage, minerals, and some form of moisture, be available the year around, relatively free of snow and within a short distance of the required topographic conditions. The mountain sheep are basically grazers rather than browsers; therefore, in general they seem to prosper better where the forage is grassy or herbaceous rather than woody. A source of mineral matter, chiefly phosphorous and calcium, seems to be a necessity. Moisture in some form is a requirement although the sheep seem to satisfy this need remarkably well by eating snow and succulent vegetation.

LATITUDE

It appears necessary to suspect a probable southern limit to mountain sheep habitat, since the animals do not seem to distribute themselves naturally south of twenty-five degrees north latitude. Assuming such a latitudinal barrier for the northern hemisphere, it is quite likely that areas south of twenty-five degrees south latitude would be satisfactory from a latitudinal standpoint. The blue sheep is said to have been successfully introduced into New Zealand.

SUMMARY

To summarize, therefore, the ecological niche of the mountain sheep consists of temperate to subarctic conditions which provide relatively continuous cliffy or broken topography. Forage (preferably grassy or herbaceous), water, and minerals must be available comparatively free of snow, and either among or immediately proximal to the required physiographic conditions.

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A Comparative Study of the Eyes of Some Falconiform and Passeriform Birds[1]

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The results of a comparative study of the morphology of the eyes in two orders of birds are presented in this paper. The species studied each belong to a different family, possess different modes of life, obtain their food differently, nest in different situations, and spend most of their lives in different layers of separate ecological associations. Six species were examined for this study. The Passeriform birds are: the house sparrow, *Passer domesticus,* of the family Ploceidae; the mockingbird, *Mimus polyglottos,* representing the family Mimidae; the meadowlark, *Sturnella magna,* of the family Icteridae. The Falconiformes are: the turkey vulture, *Cathartes aura,* of the family Cathartidae; the sparrow hawk, *Falco sparverius,* representing the family Falconidae; and the red-tailed hawk, *Buteo jamaicensis* (= B. borealis), of the family Accipitridae.

A major difference in the life habits between the two orders might be pointed out. The species belonging to the order Falconiformes usually spot their food from a distance considerably greater than that of the passeriform species, and only the sparrow hawk need fear an attack from raptorial predators. Those species belonging to the order Passeriformes, however, have two primary uses for their eyes; first, searching for food usually from relatively much closer distances and second, keeping a constant lookout for predators.

Appearance of the Eye

Externally the eye of a bird is very misleading as to its size. Since the eyelids cover all of the eye, except the cornea, and the sclera is nowhere in view, the eye lends the impression of being small, whereas, in reality, the eye is proportionately very large in comparison with the eyes of other vertebrates. The iris of the house sparrow is brown. The position of the eyes on the side of the head gives the impression that binocular vision would be impossible and in observing the actions of sparrows it is noted that they seem almost always to cock their heads to one side when examining an object intently. Yet it must be mentioned that live birds occasionally show the ability to apparently converge both eyes forward enough as to perhaps bring the temporal portions of the retina of both eyes to bear on relatively distant objects.

The eye of the mockingbird appears to be somewhat more laterally placed

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than that of the house sparrow, with perhaps even more power of convergence. The iris is yellow or straw colored in adult birds, and brown in young birds which still have their juvenal plumage.

In the meadowlark the eye is placed perhaps less laterally than the previous two birds. The color of the iris is brown.

The eye of the turkey vulture is likewise placed laterally rather than forward as in other members of the Falconiformes. The iris is brown in some specimens and gray in others, perhaps as another result of obtaining juvenile specimens.

The eyes of both the sparrow hawk and the red-tailed hawk are placed forward compared to those of most birds, the owls excepted, and their convergence plus the addition of a temporal fovea makes it possible for these birds to bring both eyes to bear on near objects.

This binocularity has a definite purpose in the hawks, for while good depth perception is needed in other birds, it is absolutely necessary for the survival of the species among most falconiform birds. A hawk with poor depth perception would either pull out of its "stoop" (dive for prey) too soon and miss the prey, or if the prey be on the ground the hawk might pull out of its dive too late, possibly resulting in serious injury or death. As might be expected, well developed accommodation is also a prime requisite for the depth perception requirements in the hawks for the binocularity attained is to no avail if the object cannot be constantly in sharp focus on the retina.

The iris of the sparrow hawk is brown. The iris of the redtailed hawk is yellow in juveniles, and brown in adults. The eyes of both of the hawks examined are shaded from above by the projection of a supra-ocular bone. This bone is not found in any of the other species examined.

The angle between a perpendicular plane passed through the longitudinal axis of the head and a line drawn through the center of the cornea and the fovea indicated some differences in the visual angle of the species examined. Since the angle sometimes varied a few degrees between the right and left eye it must be pointed out that the specimens examined were not in a living or fresh condition, but had been fixed in Perenyi's fluid and the angles may possibly not be the same as they would be in a living bird with its eyes at rest. Table 1 lists the angles in degrees for each eye and each species.

TABLE 1.—The visual angle*

	Right eye		Left eye	
	central fovea	temporal fovea	central fovea	temporal fovea
House sparrow	49°		49°	
Mockingbird	53°		55°	
Meadowlark	45°		45°	
Turkey vulture	45°		45°	
Sparrow hawk	49°	38°	46°	34°
Red-tailed hawk	31°	15°	31°	16°

* The visual angle is that angle that lies between a perpendicular plane passed through the longitudinal axis of the head and a line drawn through the center of the cornea and the fovea.

It can be seen from this table that the visual angle of the central fovea is widest for the mockingbird, with the house sparrow and the sparrow hawk next, is followed closely by the meadowlark and the turkey vulture, the red-tailed hawk having the narrowest visual angle of all the species examined, for both the central and temporal foveae.

An opthalmoscopic study of the eyes of the species examined showed only slight variations in the fundus. The eye ground varied in color from light gray in the meadowlark through a light blue in the house sparrow, the mockingbird, and the turkey vulture, to a pale blue green in the sparrow hawk and the red-tailed hawk. The pecten varied somewhat in size, as will be discussed below, but was consistently dark brown in color in all species examined. The free surface of the bridge of the pecten appeared pitted. The central fovea appeared somewhat deeper in the sparrow hawk and the red-tailed hawk and the circle surrounding the fovea, limiting the area centralis, was slightly ventrally excentric, and also appeared sharper than in any of the other species examined. The temporal fovea of the hawks was difficult to examine and keep within the field of the opthalmoscope, consequently no effort will be made to describe it. However, it should be mentioned that no distinct line was seen joining the two foveae as described by Wood (1917) in various species of Falconiformes. The areas and foveae of the remaining species examined were essentially similar, differing only slightly in their displacement from the dorsalmost point of the base of the pecten (to be described later). The surface of the cornea was scratched in all of the specimens examined for this study. This condition was not found in an examination of the surface of the cornea of the Australian parakeet, *Melopsittacus undulatus*, which had been kept in captivity. Also it was noted that there were fewer scratches on the corneae of the red-tailed hawk than of the other wild species examined.

THE EYE AS A WHOLE

The eye of a bird has a distinct shape when compared with the human eye, in that there is a strongly defined concavity in the ciliary region of the general outline of the eye. This concavity is most strongly marked in the eyes of the red-tailed and sparrow hawks, it is the shallowest in the house sparrow and the turkey vulture, while in the mockingbird and the meadowlark it is intermediate.

The hawks seem to show relatively longer eyes than the other four species which exhibit a tendency toward flattening in an antero-posterior direction. The actual depth or length (the distance from the apex of curvature of the sclera) and the naso-temporal diameter of the eyes of each species have been taken *in situ*. The results are listed in table 2. Since the proportions were determined from preserved specimens with the aid of a pair of fine dividers the measurements were taken only to the nearest half millimeter. All deviations noted between the eyes of different specimens of the same species were within the limits of error of this method, consequently no mean or standard deviation was computed.

The results of table 2 bring out absolute differences in the size of the eye between the species. From the standpoint of visual acuity this is of

TABLE 2.—Absolute dimensions (in mm) of the eye

	Corneo-foveal depth (eye length)	Naso-temporal diameter
House sparrow	7.0	7.5
Mockingbird	10.5	12.0
Meadowlark	10.0	11.5
Turkey vulture	19.0	22.0
Sparrow hawk	13.5	16.5
Red-tailed hawk	25.0	30.0

real importance, for in eyes an absolute increase in size usually results in an increase in visual acuity. However, these dimensions fail to illustrate variations of adaptive and taxonomic significance as do the proportions in the following table.

The proportions in table 3 are the ratio of the depth of the anterior chamber, the thickness of the cornea, the thickness of the lens, and the depth of the vitreous chamber, to the cornea-foveal length of the eye. The cornea-foveal length of the eye was selected for a standard, as that measurement least likely to vary relative to absolute differences in the size of the eyes. Variation in this length would depend primarily on a variation of optical density of the lens, aqueous humor, and cornea and the curvature of these structures. Chard and Gundlach (1938) found that the effective index of refraction of the cornea, aqueous humor, and lens of the homing pigeon was 1.05; the effective index for humans is roughly the same, 1.07. Thus, it was felt that if two such divergent eyes as above compared differed so slightly in effective refractive indexes of their optics, then probably the difference among closer related forms would, if anything, be even less. Admittedly, there are differences in the curvature of the cornea and lens between the species examined and these differences must be considered when interpreting the proportions. These proportions are the results of the measurement of ten different slides from as many specimens as were available.

Table 3.—Comparative proportions of the eye

Mean proportions	House sparrow	Mocking-bird	Meadow-lark
Depth of Anterior Chamber	11.3±1.74	9.5±3.76	8.3±.89
Thickness of Cornea	55.6±6.28	65.7±2.96	49.3±2.40
Thickness of Lens	2.5±.37	3.0±.40	3.1±.66
Depth of Vitreous Chamber	2.1±.29	1.9±.01	1.9±.18

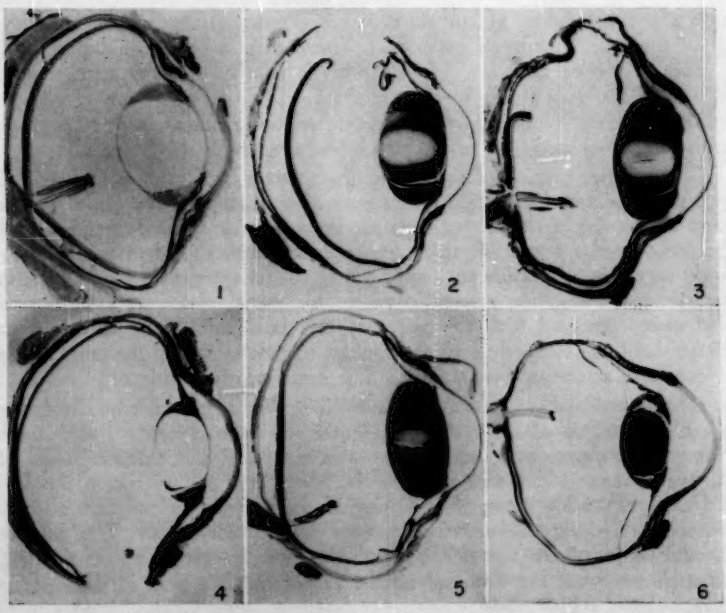
Mean proportions	Turkey vulture	Sparrow hawk	Red-tailed hawk
Depth of Anterior Chamber	8.8±.24	6.8±.51	5.1±.06
Thickness of Cornea	30.1±9.80	78.0±8.36	47.5±16.10
Thickness of Lens	3.8±.96	3.4±.19	4.0±.83
Depth of Vitreous Chamber	1.7±.05	1.8±.05	1.9±.05

The proportions of table 3 seem at first glance to have no common theme until the major factors, the development of the optics and the distances, are considered. It can then be pointed out that the anterior chamber of the sparrow hawk and the red-tailed hawk is significantly deeper, relatively speaking, than in the rest of the birds examined. While the lens of the house sparrow is significantly thicker (relatively) than the lens of the red-tailed hawk, there is no such difference between the other species. On the other hand, the lack of a statistically significant difference between the relative depths of the vitreous chambers of the species examined indicates the similarity in proportions of that portion of the eye behind the lens and ciliary structures. It will be shown later that the house sparrow possesses a low degree of curvature of its cornea, while that of the red-tailed hawk is relatively sharply curved.

ANTERIOR PORTION OF THE EYE

The anterior portion of the eye includes all structures which lie anterior to a plane passed vertically through the diameter of the eye in the region of the ora. In the house sparrow the anterior portion of the eye is outstanding for the relatively large size of the lens and the shallowness of the anterior

PLATE 1



Figs. 1-6.—Photograph of a horizontal section through the center of the eye. To facilitate comparison the photographs of the eyes of the smaller birds have been enlarged to equal the enlargements of the larger birds. 1. House sparrow; 2. Mockingbird; 3. Meadowlark; 4. Turkey vulture; 5. Sparrow hawk; 6. Red-tailed hawk.

chamber. When a horizontal section (plate 1, fig. 1) is passed through the eye it can be seen that both nasal and temporal sides of the eye are very nearly symmetrical. There is a low degree of curvature to the cornea. The iris is relatively thickened, especially at the base. Most of this thickening is in the stroma and muscles of the iris.

The mockingbird (plate 1, fig. 2) has a relatively somewhat smaller lens, and a deeper anterior chamber than in the house sparrow. There is a greater curvature of the scleral ossicle in the nasal region. There is a slightly greater degree of curvature to the cornea. The iris is relatively thickened, but its anterior epithelium stains very lightly.

The meadowlark (plate 1, fig. 3) is similar to that of the mockingbird with approximately the same degree of asymmetry between the nasal and temporal sides, and with about the same relative amount of curvature of the scleral ossicle on the nasal side. The cornea is considerably thicker (see table 3), but has about the same degree of curvature as in the mockingbird. The lens is relatively flatter and the iris is not as thickened as in either of the preceding passerines.

The anterior portion of the eye of the turkey vulture (plate 1, fig. 4) is remarkable for its similarity to the passeriform birds previously described, and for its disparity with the sparrow hawk and the red-tailed hawk. The lens of the turkey vulture is similar in shape to that of the house sparrow; both have a greater amount of curvature to the vitreous surface of the lens than all of the other specimens examined. The cornea is relatively thicker, with a lower degree of curvature, while the iris is relatively thinner than the iris of any of the passeriform species examined. Definite spaces are to be seen within the scleral plates, although they are relatively not as large as they are in the other two species of falconiform birds.

The anterior portion of the eye of the sparrow hawk (plate 1, fig. 5) is typical of the anterior portion of the eyes of most falconiform birds. There is an abrupt rise of the cornea from the limbus giving a sharper curvature to the cornea and a greater depth to the anterior chamber. The cornea is relatively very thin. There is an inward tilt of the lens toward the nasal side of the eye and a resulting greater length of the scleral plates on the temporal side when compared with the plates of the nasal side. The lens is more flattened antero-posteriorly with the vitreous surface exhibiting the same degree of curvature as the aqueous surface. The iris is relatively thinner.

The red-tailed hawk (plate 1, fig. 6) is similar to the sparrow hawk but is easily distinguished from all of the other species examined for this study. The greatest degree of asymmetry between the nasal and temporal sides of the eye is seen in this species. Likewise, there is a greater tilt to the lens and a corresponding greater lengthening of the temporal scleral plates. The cornea is relatively thicker with an even sharper curvature. The anterior chamber is relatively the deepest and the lens is relatively the thinnest, although somewhat less flattened on the vitreous surface than in the sparrow hawk.

Table 4 expresses the degree of curvature of the cornea of the birds examined, expressed inversely as the radius of curvature. In determining the degree of curvature of the corneae, a projection was made of the cornea

TABLE 4.—Corneal curvature

	Radius (in mm) of curvature of the cornea
House sparrow	60
Mockingbird	58
Meadowlark*	....
Turkey vulture	67
Sparrow hawk	57
Red-tailed hawk	53

* In preparation of the slides, no meadowlark corneae were without artifactual aberrations.

from a section taken through the center of the eye. The corneae were projected onto a piece of paper in varying magnifications according to the size of the eye, in order to equalize the distance from limbus to limbus to 100 millimeters, and then the conjunctival curve was traced. Three chords were then described for each arc and their perpendicular constructed. In this manner the radius of curvature for each cornea was determined by measuring the distance from the point of intersection of the perpendiculars to the arc. Thus the degree of curvature of the cornea is inversely proportional to its radius of curvature. After tracing the curve of the cornea from one slide, other slides were then placed in the projector to determine if the curve traced was representative of the species. In all cases the deviations from the traced curve were too slight to be outside the margin of error inherent in the method. Consequently the curve was traced for only one slide and no mean was determined.

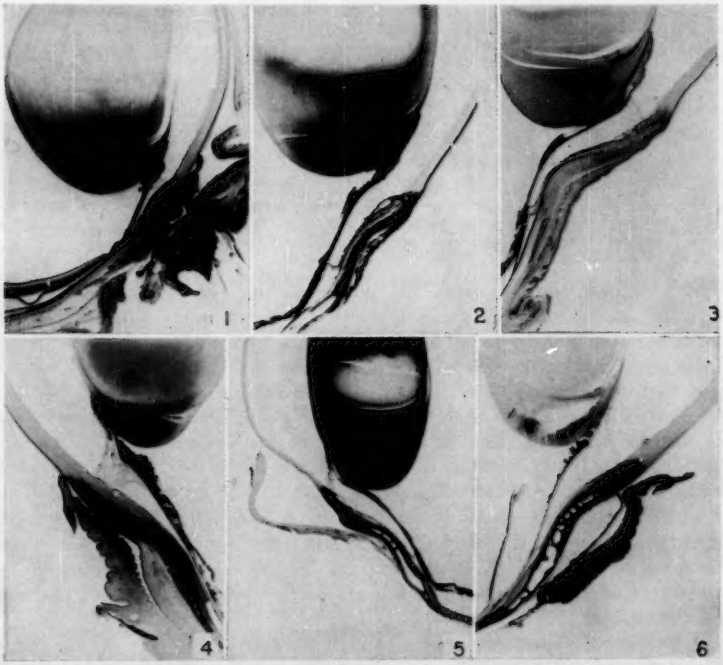
The general appearance of the anterior portion of the eyes of the species examined gives the impression of a strong similarity between all the passeriform birds and the turkey vulture of the order Falconiformes. Likewise, a strong similarity may be seen between the two remaining falconiform birds. The most obvious difference between the two groups is seen in the greater degree of asymmetry between the nasal and temporal portions of the eye as exhibited by the red-tailed and sparrow hawks.

CILIARY REGION

The ciliary region of the eye is that region encircling the circumference of the lens and containing most of the structures of accommodation.

In the house sparrow the ciliary region (plate 2, fig. 1) is relatively short and thick, a fact which can be seen in the size and shape of the scleral ossicles, and in the amount of connective tissue surrounding them. The ciliary musculature is fairly heavy and will be discussed in detail below. The canal of Schlemm is quite small and in many cases nearly invisible. On the dorso-temporal side, just posterior to the limbus, the conjunctiva and the underlying connective tissue of the sclera form a small flange, the free edge of which bends sharply away from the cornea. The probable function of this flange is that of diverting away from the cornea excess fluid and foreign particles that are pushed toward it in front of the nictitans as it is swept across

PLATE 2



Figs. 1-6.—Photograph of a section through the ciliary region of the eye. To facilitate comparison the photographs of the eyes of the smaller birds have been enlarged to equal the enlargements of the larger birds. 1. House sparrow, nasal quadrant; 2. Mockingbird, nasal quadrant; 3. Meadowlark, temporal quadrant; 4. Turkey vulture, nasal quadrant; 5. Sparrow hawk, nasal quadrant; 6. Red-tailed hawk, nasal quadrant.

the cornea. The pectinate ligament of the house sparrow is of moderate development, while the zonule of Zinn is inconspicuous and difficult to detect in histological sections.

The ciliary region in the mockingbird (plate 2, fig 2) is intermediate in length and fairly thin. This thinness can readily be seen in the thinness and length of its scleral ossicles and in the moderate development of the ciliary muscles. The canal of Schlemm is large and well developed on both temporal and nasal sides of the eye. The temporal flange is well developed as are the pectinate ligaments, but the zonule is only slightly better developed.

The meadowlark possesses a ciliary region (plate 2, fig. 3) similar to that of the mockingbird but it is also the least concave of all. The ciliary musculature of this species is slight as is the development of the zonule. There is only a moderate development of the pectinate ligament and the canal of Schlemm, but the temporal flange is well developed.

In the turkey vulture the ciliary region (plate 2, fig. 4) is elongate but

much thickened. This thickening is not a result of a thickening of the scleral plates, which in this species are long and thin and strongly curved, possessing hollow spaces within them, but rather of an increase in the amount of connective tissue surrounding the ossicles and filling in their external concavity. The ciliary musculature is moderately developed, but the canal of Schlemm is very well developed as are also the pectinate ligament and the fibers of the zonule of Zinn. There is a moderate development of the temporal flange and a moderate development of an enlarged body of connective tissue lying under the conjunctival epithelium beneath the nictitans on the nasal side of the eye. This body of connective tissue is somewhat less developed on the temporal side of the eye. This body contains only a slight amount of adipose tissue.

The sparrow hawk possesses a relatively long thin ciliary region (plate 2, fig. 5) with a well developed scleral ring. Each of the scleral plates has within it well developed compartments which are filled with adipose tissue. Interestingly, every one of the eyes of the sparrow hawk showed an enlargement of one of the posterior compartments or spaces within the ossicle in this region. The canal of Schlemm is well developed as is also the pectinate ligament and the zonule. The ciliary musculature is strong but the temporal flange, so well developed in the preceding species, is here very small. The connective tissue body found in the turkey vulture becomes a fat body in this species and is well developed on both nasal and temporal side of the eye.

Essentially all of the significant structures of the ciliary region reach their greatest development, both absolutely and relatively in the eye of the red-tailed hawk (plate 2, fig. 6). In shape and development the structures are all very similar to those of the sparrow hawk with the exception that the fat body beneath the conjunctival epithelium is much better developed in the red-tailed hawk on the nasal side of the eye than on the temporal side.

It is apparent that there is a decided difference in the size and shape of the ciliary region among the two hawks, the vulture, and the passerine birds of this study. The ciliary region in the latter group is thickened (except in the mockingbird) and possesses thin, comparatively small, scleral plates. Also, a point that was not brought out previously, the apex of the curvature of the scleral plates of the passeriform birds corresponds roughly with the equator of the lens in position, while the apex of curvature of the scleral plates of the falconiform birds corresponds approximately with a plane passed through the diameter of the eye just vitread of the lens. A circumciliary fat body lies just beneath the conjunctival epithelium in the falconiform birds; this body is apparently not found in the passeriform birds. A possible use of this fat body, beyond simple fat storage, could be insulation for the eye, for all of the specimens of the red-tailed hawk and most of the specimens of the sparrow hawk were secured in the late fall and winter months. All of the other specimens were secured during the summer season and none except the turkey vulture (as described below) exhibited this fat body. Whether the body is found in the order Falconiformes only during the winter months is unknown. Its description could not be found in the literature. The pectinate ligament is well developed in all the species but the zonule of Zinn is apparently best developed in the larger species. The canal of Schlemm appears well developed in all species except the house sparrow.

PECTEN

In the house sparrow the pecten is 4 mm long at the base and 2.75 mm long at the bridge. Its height at the highest point is 2.5 mm. There are 20 folds in the pecten of the sparrow. The pecten in the mockingbird is 6 mm long at its base and 3.5 mm long at the bridge. Its greatest height is 4 mm. The number of folds given by Thompson (1929) is 26. This study revealed only 22 folds. The meadowlark has a pecten that is 6.25 mm long at the base and 3 mm long at its bridge, with a maximum height of 3.5 mm. The number of folds is 25. In the turkey vulture the pecten is 7 mm long at its base, 5.15 mm long at the bridge, and 6 mm long at its greatest height, and has only 10 folds. The pecten of the sparrow hawk is 6 mm long at its base, 5.25 mm long at its bridge, and 5 mm long at its greatest height. The number of folds is 15. The red-tailed hawk has a pecten that is 10.5 mm long at its base, 9 mm long at its bridge, and 6.5 mm at its greatest height, and has 16 folds.

Table 5 illustrates the proportionate size of the pecten, relative to the corneo-scleral length of the eye. The final equation gives the approximate average surface area in inverse ratio to the corneo-scleral length of the eye, of one side of the pecten, discounting the folds.

Since the measurements were determined from preserved specimens with the aid of a pair of fine dividers, the measurements were taken only to the nearest one-half millimeter. All deviations noted between the eyes of different specimens of the same species were within the limits of error of this method, consequently no mean or standard deviation was computed.

In the past, writers have intimated that the degree of development of the pecten was directly proportional to the number of folds it possessed. It was felt by this writer that the number of folds is only one of the factors in the relative development of the pecten. The number of folds may be large and the relative size of the pecten reduced as in the mockingbird, thereby nullifying to some degree the amount of surface presented to the vitreous. It can be seen that the meadowlark has the greatest number of folds, with the following species arranged in descending order: mockingbird, house sparrow, red-tailed hawk, sparrow hawk, and lastly, turkey vulture. The arrangement of the species according to the relative approximate average surface area of one side of the pecten (discounting the folds) follows in descending order: house sparrow, sparrow hawk, meadowlark, turkey vulture, red-tailed

TABLE 5.—Comparative proportions of the pecten

	Basal length	Length of bridge	Height	$\frac{BL + LB \times H}{2}$
House sparrow	1.75	2.55	2.80	6.02
Mockingbird	2.50	3.00	3.76	10.34
Meadowlark	1.60	3.34	2.86	7.06
Turkey vulture	2.72	3.46	3.16	9.76
Sparrow hawk	2.25	2.58	2.70	6.52
Red-tailed hawk	2.38	2.78	3.82	9.85

hawk, and lastly, mockingbird. The results seem to indicate significant trends in the relative degree of development of the pecten (to be discussed in CONCLUSIONS). It will be seen that the number of folds in the pecten of falconiform birds is consistently lower than that of passeriform birds. The surface of the bridge of the pecten of all of the species was parallel to the surface of the lens closest to it, and very nearly perpendicular to the plane of the pecten. This condition also would seem to refute Thompson's (1929) dark mirror theory, because all rays, if reflected, would most likely be reflected through the lens and the cornea. The difference in the number of folds in the mockingbird could be due to geographical variation. The subspecies described by Thompson (1929) was *M. polyglottos leucopterus,* while the birds examined for this study were *M. p. polyglottos.*

LENS

Previously, the general shape and the relative size of the lens and annular pad as a whole were discussed under the section ANTERIOR PORTION. It remains, therefore, to give a more detailed description of the lens and present some absolute measurements in tabular form.

The lenticular portion of the lens of the house sparrow is more spherical than that of the other species studied. The space between the annular pad and the lenticular portion of the lens is relatively thin and is beveled more anteriorly. The lens of the other species follows a similar pattern except for that of the turkey vulture which is similar to the house sparrow. The lens of the other species is more flattened, being flattest in the sparrow hawk and the meadowlark and somewhat more rounded in the mockingbird and red-tailed hawk. The space between the annular pad and the lenticular portion of the lens tends to increase relatively with an absolute increase in size of the eye.

Table 6 lists an average of actual measurements taken from horizontal sections through the center of the lenses.

The temporal side of the annular pad of the lens is consistently thicker than the nasal side in all of the species except the turkey vulture, in which both sides are equal. Walls (1942) feels that, in general, the thickness of the annular pad is correlated with the capacity for accommodation. If this be so, then the greater thickness of the annular pad on the temporal side of the eye might be correlated with the rather general increase in ciliary muscu-

TABLE 6.—Comparative dimensions (in mm) of the lens

	Diameter of lens and annular pad	Diameter of lens	Diameter of annular pad	
			Nasal	Temporal
House sparrow	4.25±.54	2.95±.19	.60±.10	.69±.07
Mockingbird	6.00±.47	4.18±.57	.89±.60	.96±.93
Meadowlark	6.50±.33	4.20±.09	1.09±.06	1.16±.22
Turkey vulture	8.50±1.2	6.48±1.2	1.02±.05	1.02±.24
Sparrow hawk	7.50±.19	4.83±.06	1.32±.06	1.35±.14
Red-tailed hawk	13.00±.63	9.05±1.0	1.94±.49	2.01±.31

lature on the same side of the eye. And also the equality of the annular pad in the turkey vulture could be an expression of extra ciliary musculature in that species in the form of the dorso-nasal ciliary muscle (to be described below).

The diameter of the annular pad as a percentage of the diameter of the lens plus its annular pad, varies between the species. In the house sparrow it is 30.59%±2.76, in the mockingbird 30.59%±4.92, in the meadowlark 34.66%±2.78. In the turkey vulture the relative diameter of the annular pad is 24.27%±7.36, while in the sparrow hawk it is 35.66%±3.94. In the red-tailed hawk it is 30.44%±9.54. This means that the annular pad is best developed in the sparrow hawk and least developed in the turkey vulture while all the rest are intermediate. The only significant difference found was that between the turkey vulture and the sparrow hawk, it was felt that if a larger sample had been available, a significant difference would have appeared between some of the other species.

CILIARY MUSCLES

In the examination of the ciliary muscles, there were slides on which, with liberality, one could have interpreted the presence of Muller's muscle; but as long as there was some possibility that the 'separate' muscle seen could have been a separation of Brück's muscle as a result of fixation, it was thought best to be conservative, and the 'two' muscles were called Brück's muscle.

The house sparrow possessed both Crampton's muscle and Brück's muscle and both were relatively well developed. In this case no separate muscle bundle was seen that could have been called Müller's muscle. The mockingbird possessed three ciliary muscles: Crampton's muscle, Brück's muscle and a temporal ciliary muscle (to be described later). The Crampton's and Brück's muscles were moderately developed, but the temporal ciliary muscle was not strongly developed.

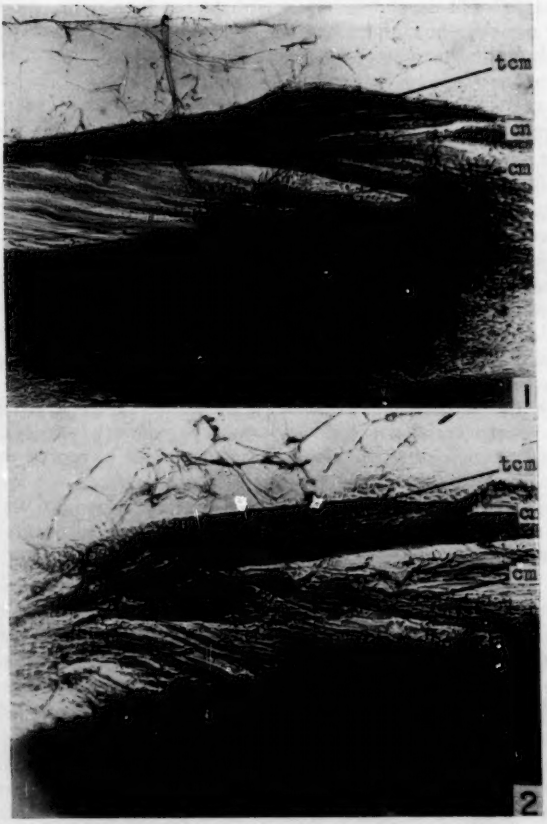
In the meadowlark little distinction could be drawn between the bundles of the ciliary muscles and it was, therefore, felt that there was only one.

The turkey vulture probably possesses only three ciliary muscles. They are Crampton's, Brück's, and a dorso-nasal ciliary muscle. All of the muscles are moderately developed with an extension of muscle fibers between Crampton's muscle and Brück's muscle that could, with liberality, be called Müller's muscle. The dorso-nasal ciliary muscle shall be discussed later with the temporal ciliary muscle. In the sparrow hawk there are four ciliary muscles, all well developed. They are Crampton's, Müller's and Brück's muscles, and a temporal ciliary muscle. The redtailed hawk also possesses four ciliary muscles, as in the sparrow hawk, but with relatively better development, especially of the temporal ciliary muscle.

TEMPORAL CILIARY MUSCLE

A muscle was found on the temporal side of the eye of the redtailed hawk, the description of which could be found nowhere in the literature. The muscle is found in the region of Crampton's muscle and the ciliary nerves, in the ciliary region of the eye.

PLATE 3



Figs. 1, 2.—Photograph of a horizontal section through the temporal ciliary muscle. 1. Red-tailed hawk; 2. Sparrow hawk. tcm—temporal ciliary muscle; cn—ciliary nerve; cm—Crampton's muscle.

In the red-tailed and sparrow hawks this ciliary muscle (plate 3, figs. 1 & 2) has its greatest development on the temporal side of the eye. However, a few fibers of this muscle may be found on the nasal side. The fibers of the muscles are arranged radially like the other ciliary muscles of the bird's eye. The origin of this muscle is on the inner side of the scleral sheet which forms the anchorage of the pectinate ligament. The insertion of the temporal ciliary muscle is on its tendon which extends from the anterior end of the muscle, passing over the interior and exterior wall of the canal of Schlemm and attaching to the connective tissue of the sclera at the limbus, which is in

immediate contact with the internal fibers of the substantia propria of the cornea. The fibers of this muscle, which has been given the name temporal ciliary muscle, while adjacent to the fibers of Crampton's muscle, are separated from it by the tendon of Crampton's muscle and by branches of the ciliary nerve. The fibers of the temporal ciliary muscle run parallel to the tendon of Crampton's muscle and the scleral ossicle laterad to it, while the fibers of Crampton's muscle run obliquely from their origin on the connective tissue of the sclera, mediad of the scleral ossicle, to their insertion on their tendon in a direction pointing generally toward the iris.

This muscle was found in a relatively reduced condition in the eye of the mockingbird. A similar muscle, also relatively reduced in size, was found on the dorso-nasal side of the eye of the turkey vulture.

The action of the temporal ciliary muscle is probably the same as that of Crampton's muscle; that is, it is a depressor corneae. However, located as it is the action is not uniform but probably increases the curvature more on the temporal side than elsewhere. Possibly this is an added specialty in the improvement of binocular vision.

The development of the ciliary muscles has a direct relationship to the degree of accommodation the bird has. The relatively strong development of the ciliary muscle of the hawks and the sparrow as compared to the moderate development in the turkey vulture, the mockingbird, and the meadowlark probably has some degree of significance. Also the number of ciliary muscles seems to correspond roughly with the degree of development of the ciliary region and accommodation.

RETINA

The retina in the eyes of the birds examined, although not measured, is probably relatively thicker in the eyes of the smaller birds as compared with the larger. The retina of the sparrow hawk and the red-tailed hawk differs in several ways from that of the other species, but from a macroscopic viewpoint it begins to taper toward the ora at the point where the fundus makes its sharp cornead curvature, and where the retina terminates at the ora it is relatively thinner, resulting in a less well defined ora terminalis. This area or band of tapering also has another peculiarity in the two hawks. The nervous cytoplasm of this area takes on a plasma stain. This phenomenon does not occur in any of the other species, nor does it occur in the center of the fundus of the sparrow hawk and the red-tailed hawk.

A count was made of the number of visual cells in a single plane 0.1 mm long. This count was made in every case within the central (nasal) area

TABLE 7.—Visual cell counts

	Number of visual cells per 0.1 millimeter
House sparrow	27.5±3.88
Mockingbird	30.1±2.00
Meadowlark	29.5±3.70
Turkey vulture	29.7±4.44
Sparrow hawk	32.8±5.16
Red-tailed hawk	30.5±4.96

but never included those cells directly beneath the fovea. Table 7 lists the average number of visual cells for 0.1 mm of ten different counts of at least five separate slides of each of the species examined.

The similarity of the counts illustrates the close degree of uniformity in the thickness and distribution of the visual cells in the retina among these species.

A count was made of the nuclei of the layers of the retina which should, in general, indicate the degree of summation found in the different species. Table 8 lists the averages of ten nuclear layer counts made on at least five different slides. The counts were made away from any foveal influence. Walls (1942) lists a similar table except that the numbers are probably not averages, but some actual counts. For the house sparrow he lists: outer nuclei—3, inner nuclei—12, ganglion cells—2. The averages determined by this study differ by 0.1, 1.3, and 0.7 respectively. For the red-tailed hawk he lists: outer nuclei—3, inner nuclei—17, ganglion cells—2. The averages determined by this study differ by 0, 1.1, and 0. All of the variations between the results obtained in this study and those listed by Walls show the averages of this study to be higher.

It can be seen that the greatest number of bipolar cells and amacrine cells (inner nuclei) per visual (outer nuclei) cells and ganglion cells is found in the meadowlark, the sparrow hawk, and the mockingbird. However, due to considerable variation in the inner nuclear layer most of these differences are not statistically significant.

The central foveae of the species are generally similar in their appearance. The central foveae of red-tailed and sparrow hawks are the deepest of the falconiform species and the foveae of the mockingbird and the house sparrow are the deepest of the passeriform species. The foveae of the two remaining species, the turkey vulture and the meadowlark, and especially the latter, are noticeable for their apparent lack of any thickening of the retina immediately marginal to the foveae, a feature which is conspicuous in the hawks. There is an outstandingly steep pitch in the "in-dip" of the fovea of the meadowlark.

All of the species have well developed central foveae, and the sparrow hawk and the red-tailed hawk have in addition temporal foveae. There is no obvious temporal foveae in the eyes of the turkey vulture (of the same Order as the hawks).

Measurements were made of the distance between the central fovea and the nearest (dorsalmost) point of the pecten. In the hawks, which possess a temporal fovea as well as a central fovea, measurements were also made

TABLE 8.—Nuclear layer counts

	Outer nuclei	Inner nuclei	Ganglion cells
House sparrow	2.9±.20	13.3±2.12	2.7±.96
Mockingbird	4.1±1.34	28.8±6.6	4.4±1.40
Meadowlark	3.9±1.34	30.2±2.98	3.8±1.55
Turkey vulture	4.0±.88	18.7±6.64	2.8±.06
Sparrow hawk	3.1±1.32	25.3±14.9	3.2±1.56
Red-tailed hawk	3.0±0.00	18.1±7.62	2.0±0.00

of the distance from the temporal fovea to the pecten, and of the distance between the two foveae. Table 9 is a listing of these measurements. Since the measurements were determined from preserved specimens with the aid of a pair of fine dividers, the measurements were taken only to the nearest one-half a millimeter. All deviations noted between the eyes of different specimens of the same species were within the limits of error of this method, consequently no mean or standard deviation was computed.

The relative increase of the distance between the fovea and the pecten with a corresponding increase in the absolute size of the eye, shows a tendency for the fovea and pecten to occupy relatively the same position in the eye throughout the species. This seems to hold true for all but the turkey vulture in which either the pecten or the fovea or both are relatively closer together.

Beyond the ora terminalis there is an extension of the retinal epithelium over the vitreous surface of the basal plate and ciliary processes. In man this epithelium is made up of cuboidal or columnar cells, and so is most of it in birds. However, wide sections, a few millimeters anterior to the ora, in birds' eyes may have conical cells with the apex of the cone pointing vitread. The same situation was observed in slides of frogs' eyes. It is suggested in this study that this phenomenon may be a result of the tension of the fibers of the zonule, or possibly it is a vestige of serial homology related to the development of the vertebrate visual cells.

VISUAL HABITS OF THE SPECIES

It is apparent from the foregoing material that the eyes of the house sparrow possess tendencies toward a relatively myopic condition found in the lowness of the cornea, shallowness of the anterior chamber, and thickness of the lens. This tendency might be expected from the habits of the bird, which is essentially a seed eater and not given to long flights or excursions to high altitudes. The seed and whatever insects it may devour are either seen monocularly from a perch, usually not more than twenty feet above the ground, or the food is found while the bird is hopping about on the ground in its quest.

Probably most of the mockingbird's food is seen from a somewhat greater distance than that of the house sparrow. The food is primarily insect in form and, therefore, probably in motion when perceived. Though most of the food is taken from the ground or trees, occasionally food may be taken on the

TABLE 9.—Position of fovea

	Central fovea to pecten	Temporal fovea to pecten	Central fovea to temporal fovea
House sparrow	1.5 mm		
Mockingbird	2.0 mm		
Meadowlark	2.0 mm		
Turkey vulture	2.5 mm		
Sparrow hawk	3.0 mm	4.0 mm	5.5 mm
Red-tailed hawk	3.0 mm	4.5 mm	6.7 mm

wing in the manner of flycatchers. These habits require an eye of intermediate abilities with neither myopic nor hypermetropic tendencies and such an eye is probably possessed by the mockingbird, as far as this study is able to determine.

The visual habits of the meadowlark do not seem to correlate exactly with the development of its eye; a possible explanation of this will be offered later. The meadowlark spends most of its time in the open fields searching the grass for insects and possibly some few seeds. Consequently, most of its food is seen and obtained from close range.

All of the passerines have one visual habit in common, i.e., they must all be constantly alert to every moving thing both on the ground around them and in the skies above them for although predation may not be a serious threat to their species, it is a constant threat to each passeriform bird as an individual. That this is actually so, is shown for instance, by the medieval falconer who carried a shrike in a cage, the nervous habits of which told him that his hawk was within the bird's view, though beyond human vision. Or, observe the scrutiny which the common chicken gives every flying thing in the skies.

The carrion feeding habits of the turkey vulture are well known but it has long been a controversy as to the manner in which a vulture locates his food. Some have claimed that the bird possesses a keen sense of smell, while the latest trend in thinking is that the sense of sight is entirely responsible. Possibly both senses are utilized. At any rate, it is not difficult to observe the turkey vulture while circling high above, turn its head from side to side and scan the ground. That they have well developed visual acuity is nearly undeniable to the observer who has watched vultures converge from all points to a single individual which has discovered a dead animal.

The exceptional visual acuity of the hawks has long been admired by man, as have also their long accurate dives made to secure their food. It has been observed in the field that while in flight both species of hawks examined and the turkey vulture, in scanning the ground for food, turn the head to one side or the other, but seldom drop the head, as if to bring both eyes to bear on objects below them. However, it has also been observed that in a "stoop" the head is not turned to one side, but held straight, as it were, to bring both eyes to bear on the prey. Live captured hawks could seldom be induced to observe a near object with one eye. It is, therefore, felt that the probable method of eye use by wild hawks is to use the apparently more hypermetropic central fovea monocularly for scanning the ground in search of prey, while in a dive in pursuit of their prey the binocularity of the possibly more myopic temporal foveae is brought into use. Hawks probably do not see, or at least are not excited by, immobile prey. Witness the experience of the falconer in recalling his hawk by swinging the lure in a wide circle about his head. Or better, in capturing wild hawks, his use of live birds as bait, which he stimulates into action by the use of a long string whenever the hawk comes into range.

One of the feeding habits of the sparrow hawk is to sit on a wire or high pole in an open field watching for grasshoppers or small mammals, and then drop suddenly on it when one is spotted. Another feeding habit highly

characteristic of the sparrow hawk is for it to fly over a field at a height of about 20 or 30 feet and when spotting prey stop in mid-air, hovering in place for sometimes as long as a minute or two, and then dropping suddenly on its prey. As falcons, sparrow hawks are agile and swift of flight and are able to and on occasion do, pursue and capture small birds. The red-tailed hawk on the other hand, is a *Buteo,* slower and more apt to drop from its high circling habit upon some small field mammal. It should be mentioned, however, that of the stomachs examined of these birds, secured for this study on the coastal plains of Texas, most of the food seemed to be grasshoppers, although one specimen contained remains of a meadowlark.

DISCUSSION

It is apparent that there is a wide difference in curvature of the cornea and lens among the species. The house sparrow and the turkey vulture on one hand have low corneae and well curved lenses. While on the other hand, the red-tailed hawk and the sparrow hawk have highly curved corneae and relatively flattened lenses. As the effective optics are made up of the cornea, aqueous, and lens, the above two opposing structural designs optically are similar, giving relatively similar focal lengths for the size in which they are found.

Then the reason for this opposition is not an adaptation to hypermetropic or myopic tendencies (all the more evident when it is pointed out that *C. aura* probably has tendencies toward hypermetropia). The answer probably lies in the accommodation ability required by the species. A relatively low degree of accommodation is needed by ground feeding, seed eating birds, or birds which find their food from afar and slowly descend to it (the house sparrow and the turkey vulture respectively). Consequently, these birds can get along with an accommodation mechanism which acts secondarily on its optics by heaving first on the basal plate and the ciliary processes, which in turn press on the lens. However, birds such as the hawks need a relatively high degree of accommodation for reasons previously mentioned, that is, efficient binocularity and ability to keep focused on moving prey. In contrast to the house sparrow and the turkey vulture the hawks' muscles of accommodation probably act most effectively, directly on the curvature of the cornea, which has the added advantage of having a much less dense medium adjacent to it than does the lens, thus lending it a greater degree of refraction. This means that less effort on the part of the ciliary muscles accomplishes more accommodation. The mockingbird and the meadowlark represent intermediate forms, possessing a higher cornea and flatter lens than the house sparrow, yet not so much as the hawks. Likewise, their demands for accommodation are intermediate. The mockingbird is quite agile in flying through the limbs of trees and in snatching insects in flight. The meadowlark, however, apparently has no great need for the accommodation apparatus it possesses. Perhaps its presence is explainable in the arboreal habits of most of the other members of the family Icteridae to which it belongs.

It is also possible to correlate the need for accommodation among the species examined and the ratio of the diameter of the annular pad to the

diameter of the lens plus the annular pad as previously given. Here the sparrow hawk has the greatest development of the annular pad, explained by the habits of falcons in general rather than by the specialized habits which the sparrow hawk has adopted. The turkey vulture possesses the least relative development of the annular pad which can again be correlated with low capacity for accommodation. The remaining species are intermediate in the development of the annular pad and can have their degree of development explained by either adaptive evolution or phylogenetic inheritance or both.

The ciliary musculature is even more readily correlated with the need for accommodation. The greatest development and the greatest number of ciliary muscles occurs in the hawks, while the smallest number are in the house sparrow and the meadowlark. The mockingbird has probably developed the extra ciliary muscle as an aid in accommodation. However, the turkey vulture may have its relatively good ciliary musculature in order to offset a possibly phylogenetically inherited thick cornea.

The modern view of the function of the pecten is that of supplying nutrients to the vitreous chamber thence presumably to be dispensed to the retina, because in birds there is an absence of blood vessels on the vitreous surface of the retina. Since visual acuity is based on the optics of the eye plus the number of visual cells over which the image is spread plus the little understood process of summation, it would not be expected that the development of the pecten would correlate with acuity. And so it apparently does not. It might, however, be expected that the development of the pecten is correlated with the increased metabolic activity of the eyes. And thus it seems that those species which live in the open and are most strongly diurnal, are forced if they are to survive, to scan the brilliant skies constantly, from which comes the source of light and also their predators. It is these species which possess the relatively largest and best developed pectens. Conversely, the owls have relatively small pectens. The hawks and vulture mostly look earthward away from the source of light, and the mockingbird spends the brightest part of the day in the shade and protection of trees and bushes. All this indicates that there is a possibility of correlation between the degree of breakdown of photochemical cone substance by intense light rays and the development of the pecten, seemingly to furnish sufficient nutrients for the constant reformation of the cone substance.

In general, the eyes of the species examined for this study can be placed morphologically and taxonomically into three groups. The first is the passeriform group containing the house sparrow, the mockingbird, and the meadowlark. The second group is the hawks: the sparrow hawk and the red-tailed hawk. And last is the turkey vulture, which taxonomically is placed in the same Order as the hawks; the morphology of its eyes, however, more closely resembles that of the passeriform birds. This disparity between the eye of the turkey vulture and the other falconiform birds, tends to support those taxonomists who would remove the Cathartidae from the order Falconiformes.

SUMMARY

In this study a morphological comparison of the eyes of three species of passeriform birds, the house sparrow (*Passer domesticus*), the mockingbird

(*Mimus polyglottos*), and the meadowlark (*Sturnella magna*), and three species of falconiform birds, the turkey vulture (*Cathartes aura*), the sparrow hawk (*Falco sparverius*), and the red-tailed hawk (*Buteo jamaicensis*), has been made. The major differences observed were found in the development of the ciliary region and the proportions and thicknesses of the major structures, probably resulting in greater accommodation and better depth perception for the latter two forms of the order Falconiformes. The eye of the turkey vulture more closely resembled the passeriform eye. A dorso-temporal flange of the sclera in the region of the limbus is described in many of the birds. Also a circum-ciliary fat body lying just under the epithelium is described in the hawks. A temporal ciliary muscle, distinct from all other ciliary muscles is described. Its fibers run obliquely to those of Crampton's muscle and its origin, and insertion is different. An attempt was made to correlate differences in structure with differences in the habits and habitat of the Orders and species studied.

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A Revised List of Euryhalin Fishes of North and Middle America

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It has been long known that certain marine fishes enter fresh-water in addition to anadromous species that run up rivers to spawn. Günther (1880, p. 202) said: "Almost every large river offers instances of truly marine fishes . . . ascending for hundreds of miles of their course; and not periodically, or from any apparent physiological necessity, but sporadically throughout the year . . ." Ordinary faunistic surveys, which are usually made without salinity determinations, indicate that this phenomenon is more common in the tropics than in temperate regions. Nevertheless, it is common in North America and several authors have mentioned it. Marine fishes are found in the Atchafalaya River of Louisiana over 160 miles from the sea (Gunter, 1938b) and numerous marine species occur in fresh-water at Homasassa Springs, Florida (Gunter, 1942, Herald and Strickland, 1949). Bailey, Winn and Smith (1954) questioned these records but furnished others for the Gulf Coast. Odum (1953) has shown that the fresh-waters of Florida generally, including Homosassa Springs are quite high in salt content. Crabs (Gunter, 1938b) and other marine animals also enter fresh-water, but the action is much more common to fishes and doubtless takes place at all coastal river mouths to some extent. Some fresh-water fishes also descend the rivers and spend a time at sea. Myers (1938, 1949) has proposed a six division classification of fishes with regard to salt tolerance, which is particularly useful in zoogeographic studies. In this paper we are not particularly concerned with those problems.

Remarks and records in the literature on the salinity where fishes are captured are scattered, incomplete and hard to find because they are included as side issues in papers devoted to other subjects. The writer attempted to summarize the information for North and Middle America by compiling a list of the fishes of the continent which have been found in both fresh-water and sea water (Gunter, 1942). Due to the incompleteness of the literature, the help of a number of ichthyological workers was solicited. The response was gratifying and several unrecorded observations were brought to light. This paper is essentially a revision and extension of the former list.

An animal which will withstand or tolerate gross salinity changes is said to be euryhalin. There are all degrees of euryhalinity, grading from animals which can withstand little or no salinity change to those which can change from sea water to fresh-water or vice versa and live in either environment indefinitely. There are also degrees of rapidity with which animals can undergo salinity changes, but little is known of this aspect of the subject.

The term euryhalin has never been rigidly defined and any rigid definition is essentially arbitraty. The writer (Gunter, *op. cit.*) defined an euryhalin

fish as one which had been recorded from both fresh-water and pure sea water by competent observers. Only fishes falling into that category were included in the former list and in this revised list. This definition excludes several fresh-water fishes and a greater number of marine fishes which enter bay waters of low salinities. The definition includes catadromous and anadromous species and both fresh-water and marine fishes which enter the other environment occasionally and irregularly. Some fishes on the list may not be able to withstand fresh-water or pure sea water indefinitely, and for many species the matter can only be determined by experimentation.

The list was made up conservatively and species were not included unless definite evidence was forthcoming that the fish belonged in the euryhalin category as defined. In several cases there was strong ancillary evidence that species belonged on the list, but such fishes were placed in a group called *probably* euryhalin. That group is not treated here and interested readers should consult my previous paper (Gunter, *op. cit.*).

The above definition of euryhalinity depends, among other things, upon the definition of fresh-water. Probably no animal could live indefinitely in distilled water, and the term pure fresh-water is ambiguous. All land waters contain some salt and rain may range up to about 10 parts per million chloride, when it is near the sea. Soft fresh-water runs from about 0.05 to 0.07 *per mille* salt or 50 to 70 parts per million; hard fresh-water may be 0.30 parts per thousand salt. The fresh-waters of various coast lines differ considerably in salt content; on certain low lying coasts some of this salt may come from the sea and fresh-water records of marine fishes from such coasts are always suspect.

On this continent Florida fresh-waters are a special case. Odum (1953) has shown that the lower peninsula and the east coast area, almost half of the peninsula, has waters with a chloride content of 100 parts per million and sometimes more. This is over twice the chloride content of hard fresh-water which is generally about 40 parts per million. Many of the records of marine fishes in the fresh-waters of Florida are from areas where the chlorinity is 570 to 900 parts per million (Odum, *op. cit.*), which lies in the oligohaline zone. Therefore,a number of the fishes from Florida fresh-waters are not included in the following lists, because their inclusion would be at variance with the basic conceptions of the list as applied to other areas. Nevertheless, these species are marine invaders in Florida waters, and Carr and Goin (1955) have recorded the following species from Florida, which have not been reported from fresh-water elsewhere: *Dasyatis hastata* (De Kay), *Anchoa h. hepsetus* Bonnaterre, *Adinia xenica* (Jordan and Gilbert), *Diplodus holbrooki* (Bean), *Eucinostomus argenteus* Baird and Girard, *Diapterus olisthostomus* (Goode and Bean), *Eleotris abacurus* Jordan and Gilbert, *Bathygobius soporator* (Cuvier and Valenciennes), *Lophogobius cyprinoides* (Pallas), *Microgobius gulosus* (Girard), *Paralichthys albigutta* Jordan and Gilbert and *Symphurus plagiusa* (Linnaeus).

REVISIONS IN THE LIST OF EURYHALIN FISHES

The Gulf shad, *Alosa alabamae* Jordan and Evermann, and the Mississippi Valley or Gulf alewife, *Pomolobus chrysochloris* Rafinesque, are added

to the list. The former is known to be anadromous and presumably the latter is, too. It has been recorded from widely scattered points in the Mississippi Valley and Central Texas and from sea water on the Texas coast (Gunter, 1945).

Brevoortia smithi Hildebrand, of the Atlantic coast, is added to the list on the authority of Carr and Goin (1955). *Brevoortia patronus* Goode is added on the authority of Gunter and Shell (in press). *Brevoortia gunteri* Hildebrand, was recorded from full salt water in Texas, under the name *Brevoortia* sp. (Gunter, 1945). I have since taken it in fresh-water in the Mission River, Refugio County, Texas, and the species is added to the list.

The ariid catfish, *Galeichthys guatemalensis* (Günther) is added to the list on the authority of Carr and Giovannoli (1950, p. 12).

The Gulf of Mexico cyprinodontid, *Fundulus similis* (Baird and Girard), is added to the list. It is a resident of salt and brackish waters, occasionally being found in pure fresh-water. *Gambusia affinis* (Baird and Girard) is also added to the list on the authority of Hildebrand (1917).

The Pacific cod, *Gadus macrocephalus* Tilesius, is added to the list on the authority of Dr. John T. Greenbank, who saw a specimen that had been caught by an angler in the Naknek River, Alaska about one mile below Naknek Lake, which is at least 25 miles by river to the sea. The water there is purely fresh. The fish was about 24 inches long. I am indebted to Dr. Carl L. Hubbs for the information. The Atlantic cod has been reported in fresh water by fishermen, but this statement remains to be verified by an ichthyologist.

The rough silverside, *Membras martinica* (Cuvier and Valencienna), is added to the list on the authority of Gunter and Shell (in press).

The Pacific coast marine goby, *Gillichthys miriabilis* Cooper, is added to the list on the authority of A. S. Lockley (personal communication).

One eel and six gobies from the Gulf Coast are added on the authority of Bailey, Winn and Smith (1954), who carefully measured salinities at their stations. The species are: *Myrophis punctatus* (Lütken), *Eleotris pisonis* (Bloch), *Gobionellus boleosoma* (Jordan and Gilbert), *G. hastatus* Girard, *G. shufeldti* (Jordan and Evermann), and *Gobiosoma robustum* Ginsburg.

The previous list of euryhalin fishes of North and Middle America was published in four parts, with northern Mexico as the dividing line on the West coast. On the east coast the northern division ran from the Arctic to southern Florida and the southern division ran from northern Mexico to southern Panama. This four part list was arranged to show certain results which a straight list would not bring out. The Gulf of Mexico was left out, but the Gulf species are included on the list given below. As previously published, the list was an annotated one giving the reasons for including a given species and a simplified notation showing whether the fish was catadromous, anadromous, a fresh-water fish of marine ancestry, a marine fish of fresh-water ancestry or a purely fresh-water or marine species. Besides the addition of a certain species, as enumerated above, the quadruple division of the list is abandoned here and the species are given as a straight list without comment. They are grouped as catadromous, anadromous, etc. There are also some changes in nomenclature.

A List of the Euryhalin Fishes of North and Middle America, North of the Southern Boundary of Panama

A. Catadromous species

OSTEICHTHYES

APODES

Anguillidae

Anguilla rostrata (Le Sueur)

B. Anadromous species

CYCLOSTOMATA

Petromyzonidae

Entosphenus japonicus (Mertens)
E. tridentatus (Gairdner)
Lampetra ayresii (Günther)
Petromyzon marinus (Linnaeus)

OSTEICHTHYES

CHONDROSTEI

Acipenseridae

Acipenser acutirostris Ayres
A. brevirostrum Le Sueuer
A. oxyrhynchus Mitchill
A. transmontanus Richardson

TELEOSTEI

ISOSPONDYLI

Clupeidae

Alosa alabamae Jordan and Evermann
A. sapidissima (Wilson)
Pomolobus aestivalis Mitchill
P. chrysochloris Rafinesque
P. mediocris (Mitchill)
P. pseudoharengus (Wilson)

Salmonidae

Oncorhynchus gorbuscha (Walbaum)
O. keta (Walbaum)
O. kisutch (Walbaum)
O. nerka (Walbaum)
O. tshawytscha (Walbaum)
Salmo clarkii Richardson
S. gairdnerii Richardson
S. salar Linnaeus
Salvelinus alpinus (Linnaeus)
S. arcturus (Günther)
S. fontinalis Mitchill[1]
S. malma (Walbaum)
S. naresi Günther

Osmeridae

Spirinchus dilatus Schultz and Chapman
S. thaleichthys (Ayres)
Thaleichthys pacificus (Richardson)
Osmerus mordax Mitchill

ACANTHOPTERYGII

Moronidae

Morone americana (Gmelin)
Roccus saxatilis (Walbaum)

C. Fishes living in salt water, which were derived from fresh-water stock.

OSTEICHTHYES

TELEOSTEI

NEMATOGNATHI

Ariidae

Bagre marina (Mitchill)
Galeichthys felis (Linnaeus)
G. guatemalensis (Günther)

CYPRINODONTES

Cyprinodontidae

Cyprinodon variegatus Lacépède
Lucania parva (Baird and Girard)
Fundulus grandis Baird and Girard
F. heteroclitus Linnaeus
F. majalis (Walbaum)
F. parvipinnis Girard
F. similis (Baird and Girard)

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[1] The brook trout has a sea run form and is an example of a species in the last stage of evolution from an anadromous to fresh-water form.

D. Fishes living in fresh-water which were derived from marine stock.

OSTEICHTHYES
TELEOSTEI
ISOSPONDYLI
Osmeridae
Hypomesus olidus (Pallas)

ACANTHOPTERYGII
Gasterosteidae
Gasterosteus aculeatus Linnaeus

Syngnathidae
Pseudophallus starksi (Jordan and Culver)
Syngnathus elcapitanensis Meek and Hildebrand

Eleotridae
Dormitator latifrons (Richardson)
Gobiomorus dormitor Lacépède
G. maculatus Günther
Guavina guavina (Cuvier and Valenciennes)

Cobiidae
Eucyclogobius newberryi (Girard)

E. Fresh-water fishes

OSTEICHTHYES
HOLOSTEI
Lepisosteidae
Atractosteus spatula (Lacépède)

TELEOSTEI
ISOSPONDYLI
Dorosomidae
Dorosoma cepedianum (Le Sueur)

Coregonidae
Coregonus clupeaformis (Mitchill)
Stenodus mackenzii (Richardson)

EVENTOGNATHI
Cyprinidae
Mylocheilus caurinus (Richardson)

CYPRINODONTES
Poeciliidae
Gambusia affinis (Baird and Girard)
?Mollienisia latipinna Le Sueur
M. sphenops (Cuvier and Valenciennes)

F. Marine fishes

ELASMOBRANCHII
SELACHII
Carcharidae
Carcharias platyodon (Poey)

Squalidae
Squalus acanthias Linnaeus[2]

BATOIDEI
Pristidae
Pristis microdon Latham
P. pectinatus Latham

Dasyatidae
Dasyatis sabina (Le Sueuer)

TELEOSTEI
ISOSPONDYLI
Elopidae
Elops affinis Regan
E. saurus Linnaeus

Megalopidae
Tarpon atlanticus (Cuvier and Valenciennes)

Clupeidae
Brevoortia tyrannus (Latrobe)
B. gunteri Hildebrand
B. patronus Goode
B. smithi Hildebrand

[2] According to Bigelow and Schroeder (1948) the Atlantic and Pacific (commonly listed as *suckleyi*) populations are not taxonomically distinct. It has been reported from fresh water in Europe and the Pacific, although there are indications that it will not survive long in that environment.

Clupea pallasi Cuvier and Valenciennes
Lile stolifera (Jordan and Gilbert)

Dorosomidae

Signalosa petenense (Günther)

Engraulidae

Anchoa curta Jordan and Gilbert
A. lucida (Jordan and Gilbert)
A. macrolepidota (Kner and Steindachner)
A. mitchilli (Cuvier and Valenciennes)
A. parva (Meek and Hildebrand)
A. spinifera (Cuvier and Valenciennes)

Osmeridae

Hypomesus pretiosus (Girard)
Osmerus dentex Steindachner

APODES

Echelidae

Myrophis punctatus Lütken

SYNENTOGNATHI

Belonidae

Strongylura marina (Walbaum)
S. scrutator (Baird and Girard)
S. timucu (Walbaum)

ANACANTHINI

Gadidae

Gadus macrocephalus Tilesius
Microgadus tomcod (Walbaum)

ACANTHOPTERYGII

Gasterosteidae

Apeltes quadracus (Mitchill)

Syngnathidae

Syngnathus fuscus Storer
S. scovelli (Evermann and Kendall)

Atherinidae

Atherinops affinis Ayres
Menidia beryllina (Cope)
M. menidia (Linnaeus)
Membras martinica
(Cuvier and Valenciennes)

Mugilidae

Mugil cephalus Linnaeus
M. curema (Cuvier and Valenciennes)

Carangidae

Caranx hippos (Linnaeus)
C. latus Agassiz

Centropomidae

Centropomus armatus Gill
C. nigrescens Günther
C. parallelus Poey
C. pectinatus Poey
C. robalito Jordan and Gilbert
C. undecimalis (Bloch)

Lutianidae

Lutianus apodus (Walbaum)
L. argentiventris (Peters)
L. colorado (Jordan and Gilbert)
L. griseus (Linnaeus)
L. novemfasciatus (Gill)

Haemulidae

Pomadasys crocro
(Cuvier and Valenciennes)

Sparidae

Archosargus probatocephalus (Walbaum)
Lagodon rhomboides Linnaeus

Gerridae

Diapterus lineatus Humboldt
D. peruvianus (Cuvier and Valenciennes)
Eucinostomus californiensis (Gill)
Gerres brevimanus Günther
G. cinereus (Walbaum)

Sciaenidae

Leiostomus xanthurus (Latrobe)
Micropogon undulatus (Linnaeus)
Pogonias cromis (Linnaeus)
Sciaenops ocellata (Linnaeus)

Otolithidae

Cynoscion albus (Günther)
C. nebulosus (Cuvier and Valenciennes)

Icelidae

Astrolytes fenestralis (Jordan and Gilbert)

Cottidae

Leptocottus armatus Girard

Embiotocidae

Cymatogaster aggregatus Gibbons

Eleotridae

Eleotris pisonis (Gmelin)
Evorthodes lyricus Gill

Gobiidae

Clevelandia ios (Jordan and Gilbert)
Gillichthys miriabilis Cooper
Gobionellus sagittula (Günther)
G. boleosoma (Jordan and Gilbert)
G. hastatus Girard
G. shufeldti (Jordan and Evermann)
Gobiosoma bosci (Lacépède)
G. robustum Ginsburg

Echeneidae
Echeneis naucrates Linnaeus

Tetraodontidae
Canthigaster punctatissimus (Günther)
Sphoeroides annulatus (Jenyns)

HETEROSOMATA
Paralichthidae
Paralichthys dentatus Linnaeus
P. lethostigmus Jordan and Gilbert

Bothidae
Citharichthys gilberti Jenkins and Evermann
C. spilopterus Günther

Pleuronectidae
Platichthys stellatus (Pallas)

Achiridae
Achirus fasciatus (Bloch and Schneider)
A. fonsecensis Günther
A. mazatlanus (Steindachner)

DISCUSSION

The list contains 150 species. So far as the families and types of fishes that are euryhalin are concerned, the list speaks for itself and little comment is necessary. The eel, *Anguilla rostrata* (Le Sueur), is the only known catadromous species. All anadromous species are found in the temperate zone and northward. None is known from the tropics although the common lamprey, *Petromyzon marinus* (Linnaeus), has been found in the St. John's River, northern Florida (Evermann and Kendall, 1900). The striped bass, *Roccus saxatilis* (Walbaum), has been recorded from Louisiana waters by Gowanloch (1933). These are the two most southerly anadromous species known from North American waters.

It is significant that the anadromous fishes are all lower fishes, Cyclostomata, Chrondrostei and Isospondyli, with the exception of two acanthopterygian species of the family Moronidae. The predominance of lower fishes in the anadromous group holds for the whole Northern hemisphere and possibly for the whole world.

Members of the family Cyprinodontidae and the three catfishes are the only fishes of fresh-water ancestry which have permanently moved into salt water. Although euryhalin and capable of withstanding abnormally high salinities, the cyprinodontids are characteristic of bays and brackish water.

Members of the Gobioidea are the chief fishes of marine ancestry which have taken up residence in fresh-water. All over the world gobies have become established in fresh-water and it appears that gobies have been more actively engaged in moving from the sea into fresh-water than any other group in the recent era.

The two pacific syngnathids and the stickleback, *Gasterosteus aculeatus*, are probably in a transition state of adapting themselves to the fresh-water habitat. The stickleback also lives in salt water in parts of its range. The two pipefishes seem to be in a slightly more advanced stage than Scovell's pipefish, *Syngnathus scovelli*, a marine species which may be found over most of the Peninsula of Florida. An osmerid completes the group. The Atherinidae and Osmeridae have species already firmly established in fresh-water, which do not return to the sea at all, and are now apparently stenohalin fresh-water fishes. It is possible that certain Atherinidae, at least in North America, are further along as a group in invading fresh-water than the gobies. At least some atherinids are firmly established farther inland in fresh-water.

Fresh-water fishes of North America that invade the sea are only eight in

number. The two coregonids, *Coregonus clupeaformis* and *Stenodus mackenzii*, the cyprinid, *Mylocheilus caurinus*, and the poecilid, *Gambusia affinis*, are apparently very uncommon in salt water. The gar, *Atractosteus spathula*, the gizzard shad, *Dorosoma cepedianum*, and the two Mollienisias are commonly taken in salt water. The two species, *Mollienisia latipinna* and *M. sphenops*, seem to be examples of fresh-water fishes in the process of adjusting themselves to life in salt water, being somewhat less far along in the process than the kindred Fundulus species and *Cyprinodon variegatus*.

The numbers of strictly marine fishes which invade fresh-water outnumber the fresh-water fishes which invade the sea by more than ten to one. These fishes are the group which invade fresh-water aperiodically, for reasons unknown. Data showing that they greatly outnumbered fresh water fishes invading the sea were first presented in my previous paper, Gunter (1942). Since then it was discovered that Günther (1880, p. 203) came to the same general conclusion, evidently on the basis of general observations for he presented no data. He stated: ". . . we find fishes belonging to fresh water genera descending rivers and sojourning in the sea for a more or less limited period; but these instances are much less in number than those in which the reverse obtains."

Dr. C. H. Gilbert observed in general that greater numbers of the higher, specialized fishes invaded fresh-water in the tropics than was the case in northern zones, although he never published the statement (Gunter, *op. cit.*). My original four part list (*op. cit.*) was used to demonstrate the fact, but the table was badly misprinted, and *probably* euryhalin fishes were also used. Utilizing only the euryhalin fishes listed here, it is found that there are 63 euryhalin species of fishes below the Acanthopterygii north of Mexico and 47 acanthopterygian species. South of the United States there are 30 species below the Acanthopterygii and 58 acanthopterygian species. The differential presence of lower and higher types of euryhalin fishes in the north and south is a little confused by inclusion of southern Florida and the Gulf of Mexico with the northern part of the continent. The situation is much clearer on the West coast. Most anadromous fishes belong to lower groups and all of them live in northern zones. This is superficially the reason why euryhalin fishes of a lower order predominate the north and those of a higher order predominate the tropics. The real reason can only be explained on the basis of ecology, physiology, paleontology and evolution.

Table 1 is derived from the list. It gives the numbers of euryhalin fishes in the various major groups of fishes and the number of species in the same groups given by the most complete check list (Jordan, Evermann and Clark, 1930) of North American fishes. The percentage of euryhalin species is given in the last line. The percentage of euryhalin species is very high for all the lower groups except the Elasmobranchii. In round numbers the lower 12 percent of the fishes of North America contain 40 percent of the euryhalin species. This raises some interesting questions concerning physiology and paleontology.

In some respects adaptation of marine animals to salinity may be compared to thermal adaptation. Euryhalin fishes are largely lower types. Similarly, poikilothermal animals are of a lower order. Wide ranges of temperature

TABLE I.—The numbers of euryhalin fishes of North America are given for the groups of fishes shown, with the total number of species for each group listed in the check list of North American fishes by Jordan, Evermann and Clark. The last line gives the percentage of each group which is euryhalin.

	Cyclostomes	Elasmobranchs	Holosteans and Chrondrosteans	Isospondyli	Isospondyli to Acanthopterygii	Acanthopterygii
No. of euryhalin species	4	5	5	45	23	68
No. of species in check list	14	152	18	301	1,191	2,448
Percentage euryhalin	28.6	3.2	27.8	15.0	1.9	2.8

and salinity can be tolerated. Homoiothermal animals and stenohalin fishes are of a higher order. Here, however, the analogy breaks down. Although only a narrow range of body temperature change can be tolerated by homoiothermal animals, a wide range of environmental temperature is tolerated. The stenohalin fish, on the other hand, cannot stand a large salinity change.

Comparatively little is known of the physiology of euryhalin fishes. There are all intergradations of euryhalinity and as the salinity falls in the region between sea water and fresh-water there is increasingly strong selection of euryhalin animals. Those marine animals which are completely euryhalin and can enter fresh-water are the physiologically interesting fractional remainder, selectively differentiated by falling salinities. They are predominantly fishes of lower, less specialized types. This leads to the thought that possibly larger percentages of the less specialized fishes of former geological eras were euryhalin than in the case with modern fishes.

The writer (in press) has shown that marine fishes invading fresh-water, aside from anadromous species which are in a different category, are predominantly small or young specimens. Since they are species which are first spawned and apparently of necessity must undergo early development in waters of high salinity, it does not follow that they are seeking the ancestral home. Therefore, this phenomenon does not give weight to the theory that fishes originated in fresh-water. Rather, more probable, it seems that the young marine fishes invading fresh-water are following, for reasons unknown, the behavior pattern of their ancestors, the prototypes of fresh-water fishes and land animals of ages ago.

SUMMARY

Most large rivers offer instances of marine fishes entering fresh-water, and some fresh-water fishes invade the sea. The list of euryhalin fishes in North and Middle America given here is a revision of an annotated list previously published.

The list contains 150 species.

It is significant that the anadromous fishes, except for two species, are of lower, less specialized types.

The Cyprinodontidae and two catfishes are the only recent fresh-water fishes which have moved into salt water. Members of the Atherinidae and Osmeridae have moved in and established themselves in fresh-water. Gobies, the Gasterosteidae and some Syngnathidae seem to be moving in.

The number of marine fishes which go into fresh-water outnumber the fresh-water fishes which enter sea water by more than ten to one.

A greater proportion of marine fishes entering fresh-water are acanthopterygian in the tropics than is the case in temperate North America.

The percentage of euryhalin species is much greater for the lower fishes than for advanced fishes.

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A New West Mexican Prosobranch Mollusk Parasitic on Echinoids

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Shells of two kinds of minute prosobranchs apparently belonging to the Stiliferidae were taken by the writer in 1949 from sand screenings at Cholla Cove near Puerto Peñasco, Sonora, Mexico. These were duly assigned accession numbers and put to one side in the hope of obtaining better material before attempting intensive work upon them. A single poor specimen of one of these turned up in similar screenings in 1952 together with several shells of what may turn out to be a third member of the group, but it has remained for a friend, Mr. Harry R. Turver, collecting along the outer strand of the same playa early in 1954, again to find the species first referred to, this time in some numbers, alive, nestling amongst the aboral spines of the two large keyhole urchins, *Encope grandis* A. Agassiz (fig. 1) and *E. californica* Verrill, upon both of which it would consequently appear to be ectoparasitic. Both urchins

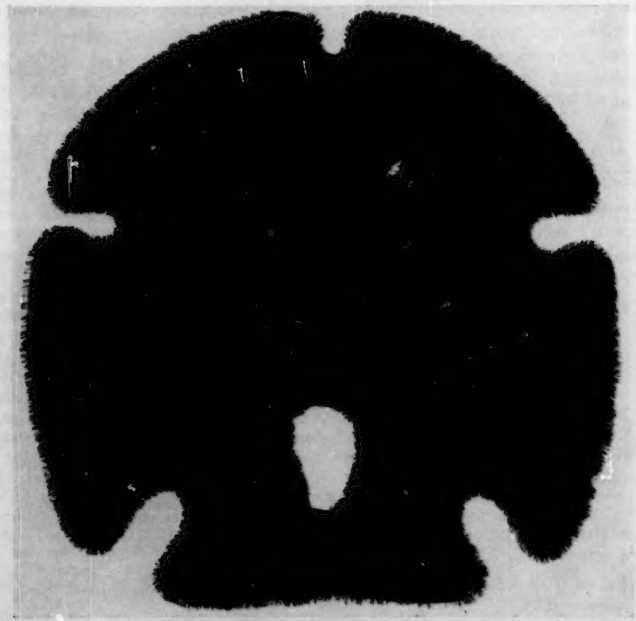

Fig. 1.—*Encope grandis* A. Agassiz.—Aboral view of specimen from Cholla Cove, Sonora, showing seven individuals of *Turveria encopendema* n.sp. *in situ* in approximately natural position; slightly enlarged.

occur associated in abundantly populated colonies on the sand-flats near low-tide line.

Through Mr. Turver's generosity in sharing his catch I am therefore now able to present a formal diagnosis of a most interesting but hitherto unpublished species, while I postpone for a little longer description of the two related forms I have mentioned in the hope that meanwhile some further stroke of good fortune will bring the hosts of these also into purview. Due acknowledgement must be tendered likewise to Mr. Ellis Rich of the College of Medical Evangelists, Loma Linda, California, for kindly supplying the accompanying remarkable photograph of one of the hosts with its possibly undesired guests skilfully arranged for the demonstration by Mr. Turver.

Turveria n. gen.

Diagnosis.—Shell minute, ovate-conic, many-whorled; smooth, except for microscopically fine spiral and incremental striae; varical marks absent; surface polished. Protoconch of several whorls, subcylindric, papilliform; later whorls rapidly enlarging; suture strongly appressed, resulting in a conspicuous "false suture" a little anterior to the true one. Aperture narrowly pyriform; outer lip thin, simple; axis imperforate.

Gen. type.—Turveria encopendema.

The genus is named for Mr. Harry R. Turver, avid collector and microscopist of South Gate, California.

Turveria encopendema n. sp.

Description.—Shell minute, ovate-conic (fig. 2). Whorls 11 to 12, the first three smooth, moderately convex, nearly cylindric and only gradually increasing, forming a small papilliform apical prolongation of the shell; later whorls much more rapidly enlarging, flattened, the last ample and barrel-like, widest near its middle, mildly subcarinate (the angle considerably more evident in young shells), thence narrowing and considerably produced in front; posterior portion of whorls strongly appressed to the suture so that an equally or even more sharply evident "false suture" becomes conspicuous a little way anterior thereto. Aperture obliquely and rather narrowly pyriform, rounded and moderately produced in front, the posterior angle acute; outer lip thin, sharp, simple; columella narrow, weakly reflected toward the base, somewhat oblique. Axis imperforate. Surface smooth, polished; without resting marks, and unsculptured except for the very delicate and cleanly traced growth-lines, which, in a good light, appear cancellated by a fine, excessively minute, spiral striation giving a faintly satiny effect. Color waxy white with a narrow subsutural band of yellowish brown which in the holotype terminates at the aperture, whereas in most of the paratypes it continues around the body-whorl as a conspicuous warm brown band.

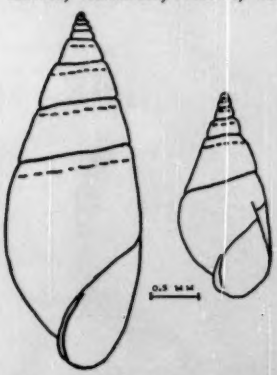

Fig. 2.—*Turveria encopendema* n. sp. Camera lucida sketch of holotype (left) and of immature paratype (Berry Coll. 23,738).

Measurement of holotype.—Alt. 4.0, max. diam. body-whorl 1.6, alt. aperture 1.7, max. diam. aperture 0.74.

Holotype.—Stanford Univ. Paleo. Type Coll. no. 7857.

Paratypes.—Berry Collections nos. 15,883, 23,738 and 23,788; others to be deposited in the collections of the United States National Museum and the San Diego Natural History Museum.

Type-Locality.—Outer strand of Cholla Cove, Bahia de Adair, Sonora, Mexico; taken in sand screenings by S. S. Berry, 11 Mar. 1949 and 13 May 1952; taken living in situ on the echinoids, *Encope grandis* A. Agassiz, and *E. californica* Verrill, by Mr. and Mrs. Harry R. Turver, 1 May 1954.

I have been able to find no described genus in which this gastropod can be placed. Of those known to me it perhaps finds nearest affiliation to *Hypermastus* Pilsbry (1899:258), but the Australian species upon which that genus is based has a cylindric-pupiform shell with so brief a one-whorled, nipple-like apex as would appear to preclude taxonomic association of the two forms congenerically. With *Hypermastus* Dr. Pilsbry synonymized the homonymous and hence invalid *Lambertia* Souverbie 1869, and placed the group in the Eulimidae, where it was subsequently retained along with other stiliferids by Bartsch (1917:354). However the general aspect of the shell and especially the papilliform apex indicate that both *Hypermastus* and *Turveria* are better cared for in the Stiliferidae where, indeed, all such forms are placed by Thiele (1929:228-230).

Another genus with which the present one should probably be compared is the (to me) rather enigmatic *Mucronalia* A. Adams (1860:301[2]), but Adams describes the shell as "*pupiformis, ovato-oblongo*", adds that "the structure of the mucro does not resemble that of the pointed apex in *Stylifer*", and refuses (perhaps wrongly) to admit a parasitic habit for his type-species. One or more of the many competent Japanese malacologists may somewhere have elaborated further on this genus, but their literature has become so vast and so few of the papers are accessible to me that my search through them for further information has thus far borne no fruit. Certainly the species figured as representative of this genus by Thiele (op.cit., fig. 230) is quite a different thing from that forming the subject of the present note.

Geographically the nearest species indicating any real relationship with *T. encopendema* is *Hypermastus cookeana* (Bartsch, 1917:354) from San Hipolito Point, and nearby localities, in Baja, California. This too has the aspect of a parasitic species although I can discover no published information which might yield a clue to the identity of its host. The stubby shell is very different in shape.

The specific name of the present species is derived from *Encope*, currently accepted generic name of both of the two known echinoid hosts, + the Gr., ἔνδημος, living in, native.

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The Ecology of the Ants of the Welaka Reserve, Florida (Hymenoptera: Formicidae)[1]

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This paper presents the results of a study dealing with ecological relationships of the ants on the University of Florida Conservation Reserve, Welaka, Florida. It is an attempt to expand the knowledge of the nesting habits and behavior of the ants of a limited area. Although similar studies on ants had been undertaken previously in other parts of the United States, especially the middle west, there still remained the opportunity to study comprehensively an area in the southeastern Coastal Plain, with its influences from both the neotropical and nearctic faunae.

In studying the ants of the Reserve, it was desired to 1) ascertain what ant forms occur on the Reserve, and to determine their quantitative relationships in each of the situations in which they are found; 2) classify these different situations from a knowledge of the qualitative and quantitative distribution of the ants in them; 3) gather as much information as possible concerning the life history and habits of the ants.

During the study much interesting information incidental to the main problem was obtained on various aspects of the ants' biology. Observations concerning the speed of movement, feeding habits, guests and parasites in the nests and on the individuals, and the hours during which foraging is done are included in an Annotated List to be published later.

The literature bearing on ants of selected regions has been, for the most part, lists or keys, including only notes as to the nesting habits of the ants concerned. Several recent papers have dealt with the ecological relationships between the ants and the environment of limited areas: Buren (1944) in Iowa; Cole (1940) in the Great Smoky Mountains of Tennessee; Gregg (1944) in the Chicago region; and Talbot (1934) also in the Chicago region. Those papers dealing with Florida ants have been four state lists (Smith, 1930, 1933, 1944; and Wheeler, 1932) and a key to the ants of the Gainesville region (Van Pelt, 1948).

Until recently, the taxonomy of ants has been based on a quadrinomial system. Several authors in the 1930's and before have made proposals to do away with this cumbersome type of nomenclature. In 1938 Creighton presented a trinomial system in which all varieties were raised to subspecific rank, and in 1944 Buren put this idea into practice for the ants of Iowa.

Finally, in 1950, Creighton published a manual on the ants of North America in which he revised his earlier concept. By discarding the category

[1] A dissertation presented to the graduate council of the University of Florida in partial fulfilment of the requirements for the degree of Doctor of Philosophy, University of Florida, 1950.

"variety" almost entirely, by synonymizing some varieties, especially color variants with the "typical" forms, and by raising several other varieties to subspecies which intergrade and replace each other geographically, he produced a nomenclatorial system consistent with that of other fields. His paper ought to have a wide influence in placing ant nomenclature on a sound basis. Several points in the present study have been simplified, and other obvious mistakes in previous nomenclature rectified by accepting his trinomial system.

In this paper literature references are given only for those papers cited in the text. No references to original descriptions or to papers dealing with synonymy are listed. The reader will be able to find these referencs, along with keys to all North American ants, in Creighton (1950).

Description of the Area

LOCATION AND PHYSICAL FEATURES

The University of Florida Conservation Reserve, where the present study was made, is a 2,180 acre tract, located on the east bank of the St. Johns River, about seventeen miles south of Palatka near the town of Welaka in Putnam County, Florida. The Reserve is situated in northeastern peninsular Florida on a portion of the state known as the Coastal Lowlands (Cooke, 1945), and is for the most part located on the Pamlico marine terrace, which is designated by its 25 foot elevation above sea level. It is approximately in the center of the rectangle formed by the lines of latitude of 29° and 30°, and those of longitude of 81° and 82°.

The Reserve varies in its topography from flat or very gently rolling lands covered with pine woods to hilly uplands supporting oak and pine, and many areas are pock-marked because of the solution of the underlying limestone. The uplands, with their sand dune appearance, are evidence that the land was once part of a marine shore line. The submergences and emergences of the Coastal Lowlands to form Pleistocene marine terraces, along with the absence of catastrophic movements in the Welaka area, as well as in all Florida, will undoubtedly prove important in consideration of the zoogeographic distribution of the Formicidae. For a complete discussion of the geology of this area, as well as other parts of Florida, see Cooke (1945).

Usually more than half of the annual precipitation falls in thunder showers during the hottest months, June to September, when rainfall averages 5 to 10 inches per month. Least precipitation occurs in late fall and again in early spring, with a monthly average of 1 to 4 inches. The annual rainfall averages under 50 inches. The weather station at Crescent City[2] recorded the total precipitation per month during the period of the present study as shown in fig. 1. For complete data on the climate of Florida from 1896 to 1926, see Mitchell and Ensign (1928).

The temperature of the area in which the Reserve is located averages about 70° F. Freezing temperatures may occur from November to March, although frost-free winters have been reported. Summer temperatures average

[2] The records of temperature and rainfall taken from Crescent City, eleven miles to the east, can be used only as general indications of conditions on the Reserve.

80° to 90°, and are at times recorded above 100°. Temperatures may vary greatly within a small area, for example, from a dense hammock to an open flatwoods. Fig. 1 shows the average monthly temperature during the period of the present study. The average length of the growing season is 300 days. The first killing frost in fall may occur in November or December; the last killing frost in spring usually occurs in February or March.

The nearest weather station recording relative humidity is at Jacksonville, where the mean annual relative humidity for 7 A.M. is 83%, while for 7 P.M. it is 76%. Records from here also indicate only the general conditions on the Reserve, since Jacksonville and Welaka are separated by seventy miles. Moreover, relative humidity varies greatly within a small area, depending upon the vegetational conditions encountered. The author has recorded relative humidity below 20% on numerous occasions in open areas on hot, sunny days.

THE SOILS AND VEGETATION

During the summer of 1948, a soil survey of the Reserve was made in order to become acquainted with the soil types present. This work was based to a great extent on the detailed survey of the area made by Laessle (1942). Where necessary, the soil-type nomenclature was brought up to date (see fig. 2). The following discussion of the derivation and texture of parent material, and of drainage, is based on Laessle's paper.

The mineral soils of the area are very probably derived from marine deposits of fine sand. No clays were found within six feet of the surface,

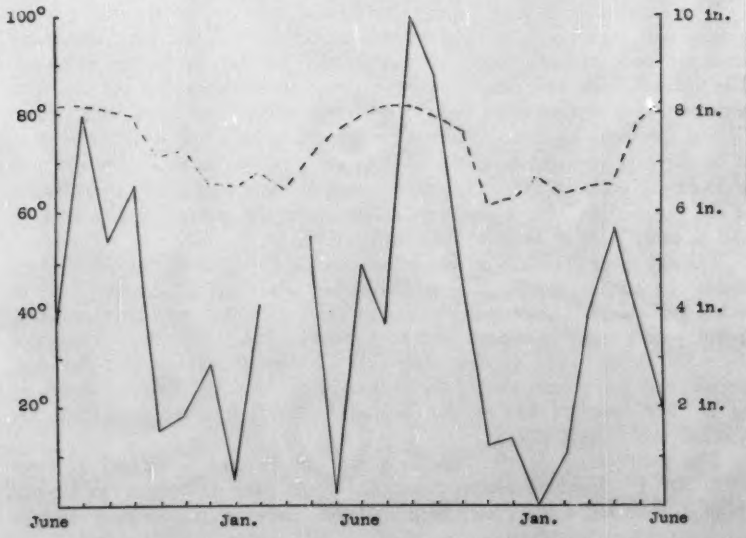

Fig. 1.—Average monthly temperature in degrees Fahrenheit (- - -) and total monthly precipitation in inches (——) at Crescent City weather station from June, 1948, to June, 1950.

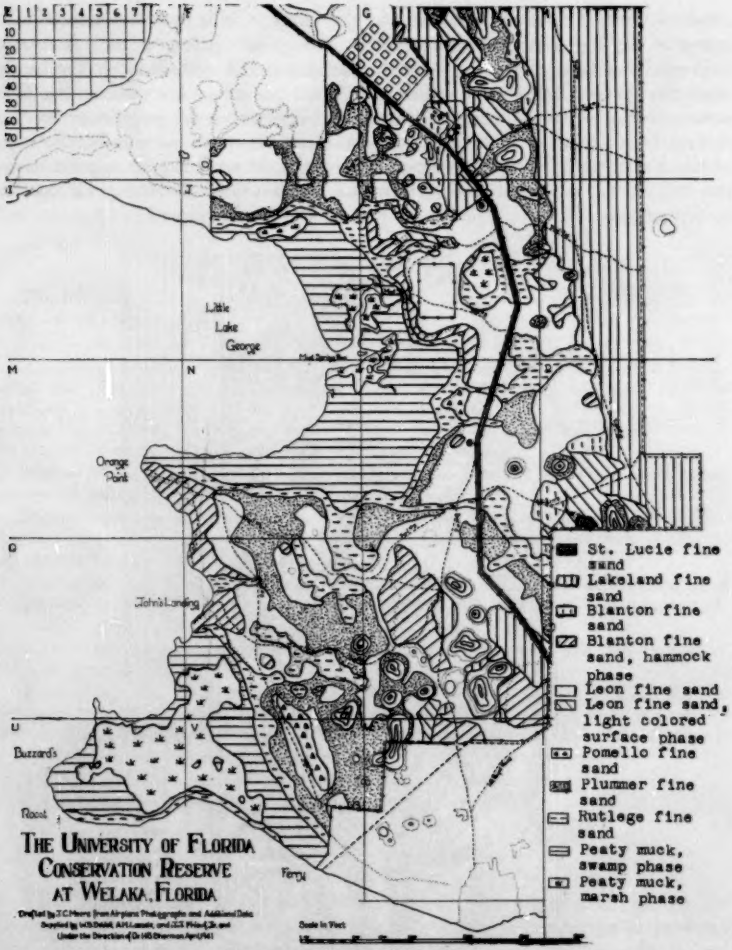

Fig. 2.—Soil map of the Reserve.

with the exception of small areas along the St. Johns River. The organic soil, peaty muck, has been laid down by the accumulation of vegetable matter in two extensive areas along the river.

Chemical analysis of the soils has been carried out only to a minor extent in nearby areas, and not at all on the Reserve.

In the rolling areas, and in other areas where the land is not entirely flat, the very sandy nature of the soil permits excellent drainage. Much of the Reserve, however, is almost completely flat, and in these areas lateral move-

ment of water is slow or negligible and the water table is near the surface. In many of the flat areas, an accumulation of organic matter, called a hardpan, is formed at varying depths beneath the surface, and in such areas during heavy rains the ground becomes supersaturated. In lower positions within the flatwoods, organic matter accumulates as a black or dark gray layer at the surface rather than as a hardpan. In contradistinction to these soils, the soils of the higher areas, with good internal drainage, do not have an organic hardpan within 42 inches of the surface and contain very little organic matter in the surface soil.

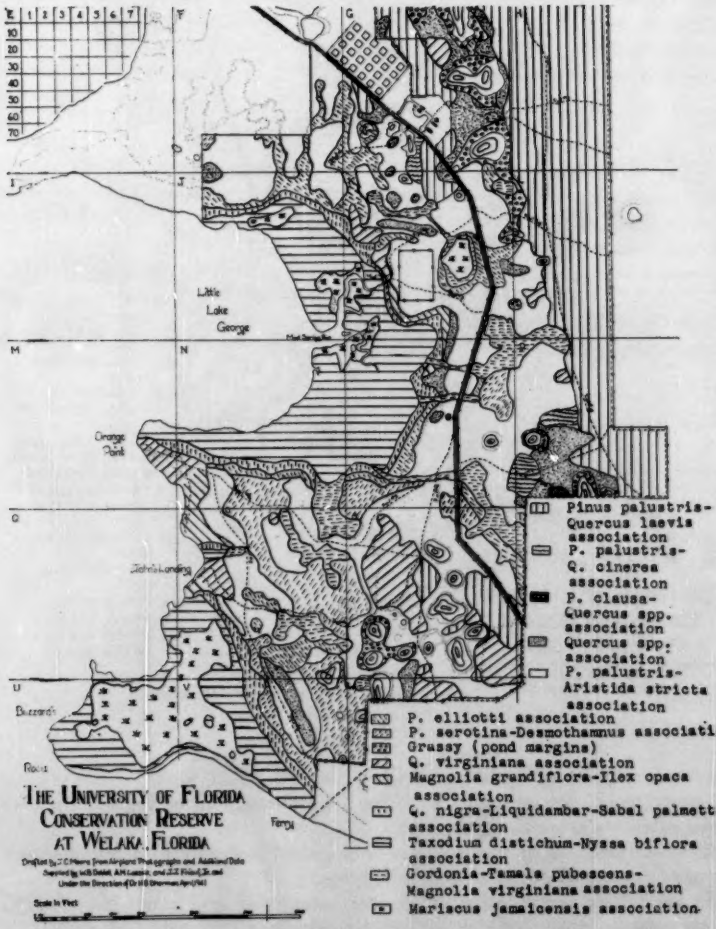

Fig. 3.—Vegetation map of the Reserve (from Laessle, 1942).

The vegetation of the Reserve (fig. 3) may be divided into four main categories, not including the various types of ruderal areas. They are 1) uplands or sandhills, 2) flatwoods, 3) hammocks, and 4) seasonally flooded areas. On the eastern side of the Reserve there is a large area of uplands supporting longleaf pine and turkey oak, and scattered in the southern portion are similar smaller areas covered with longleaf pine and bluejack oak. Various types of flatwoods form a strip, interrupted by bayheads and higher hammocks, through the center of the Reserve. Low hammocks form a strip adjacent to river swamp and marsh which border the St. Johns River.

DEFINITIONS

The following definitions of terms are given so that their use in the remainder of this paper will be clear.

Form.—Form is used here taxonomically to designate any category below subgenus.

Assemblage or species assemblage.—Species assemblage is used to designate a characteristic and distinctive aggregate of ant colonies (here of more than one form) which is contained in a given plant association, stratum, or nesting site. Such an assemblage can be separated qualitatively and/or quantitatively from any other assemblage on the basis of the type of forms present and/or their relative numbers.

Habitat.—The environment in which an assemblage occurs is its habitat, and consequently the habitat of all ant forms within the assemblage.

Stratum.—A stratum is one of the vertical levels or layers within plant associations. As used here, it is not delimited by the boundaries of any one plant association or station, but extends through all of them on the Reserve.

Nesting site.—The term nesting site refers to all nesting places of similar structure and composition, regardless of plant association boundaries. All nests in stumps, for example, are in one nesting site.

Nest.—An aggregation of one ant form physically distinct from other aggregations of the same form.

Relative abundance.—The term relative abundance is used as a measure to indicate the density and abundance of one form in a collecting station during a particular length of time relative to the abundance of any form in any station over an equal length of time. It is based on colonies, not individuals.

Station.—An area chosen as representative of a plant association.

Collection.—Applied to each nest collected or observed.

Methods of Study

Many authors have found close correlation between the distribution of the animals they studied and plant associations. On this basis they have been able to designate plant associations as the habitats of distinctive species assemblages. On the other hand, there are found to be other assemblages associated with strata. These strata may be confined to only one plant association, or they may extend through several. They have also been considered habitats. Thus an ecological hierarchy was set up with the plant associations as major habitats, and strata as minor habitats.

In order to determine if similar relationships could be expressed for the ants of the Reserve, it was first necessary to make the work on ants as comparable as possible with the work on solitary animals. It must be decided whether the ant individual or its colony will be used as the biotic unit in dealing with distribution and relative abundance. In this study the colony

in its nest, and not its individuals or their range of foraging, is considered the unit.

Among the chief reasons for basing the study on the colony rather than on the individual worker ant is that reproduction for the whole colony is generally accomplished by the queen. In this respect the workers and soldiers are not complete individuals, but generally must depend on the reproductive caste to continue the race. Food is brought back to the nest by foragers, not for their benefit alone, but for the benefit of the colony. There is cooperation among the ants of a colony, whereas there is competition among solitary animals of the same and different forms, and likewise among ant colonies of the same and of different forms. In so far as the processes of living and perpetuating the race are concerned, the colony is more complete than the individual. It is, for example, more complete than the queen, which might be suggested as the type of individual in the ant nest most closely resembling a solitary animal. Using the colony as a basis, therefore, it was proposed to determine if distinctive ant assemblages existed, and if so, by what means they could be defined.

In order to delimit ant assemblages, it was not only necessary to discover in what situations the ant forms occurred, but it was also necessary to determine as nearly as practicable the relative abundance of each form in each situation. So that this could be accomplished, it was proposed to visit plant associations (as modified in the following section) since, 1) they occur in repeated, rather uniform stands characteristic of the Welaka area, and consequently are more readily recognizable by other workers; and 2) other workers in the Welaka area and elsewhere have found plant associations to be habitats for their groups. If a correlation of plant associations and ant assemblages were found to exist, then the plant associations could be called ant habitats. If ant assemblages were found to exist in strata and in nesting sites, these too could be considered ant habitats.

It could be postulated that soils, as well as vegetation, might be a critical factor in determining where an ant form might nest. In reality, some plant associations occurred on two or more different soil types so that it seemed desirable to combine soil type with vegetation for the purpose of selecting a collecting site. All such combinations on the Reserve were designated as possible collecting localities. Several combinations were found to occupy an insignificant area and were omitted. Within each of the other soil type-plant association combinations a representative area or station was selected.

COLLECTING METHODS AND THE RECORDING OF DATA IN THE FIELD

Ants as a family are able to live in a wide variety of nesting places, although certain ant forms are quite specific in their requirements. Without a fairly complete knowledge of the ants to be dealt with, the data, especially as concerns relative abundance, could very well be invalid. It was imperative, therefore, to become acquainted as quickly as possible with the nesting habits of the ants on the Reserve, and likewise to become familiar with the plants and terrain involved.

In order to facilitate progress along this line, a preliminary survey of the ants of the Reserve was begun in October, 1947. On June 18, 1948, residence

was established on the Reserve, and concentrated collecting was begun and continued in the manner described below for somewhat over one year. The data from further collecting, carried on until June, 1950, were used to substantiate the distribution and relative abundance figures already obtained. During the period of concentrated collecting, observations were made on 3,576 nests.

Each station was visited 17 times (with additional special trips to collect one particular ant form or one particular nesting site). Visits to each station were made as nearly as possible once every month. They were continued up to (and, in reality, past) the point at which it was felt an accurate sample had been obtained, i.e., the point of diminishing returns. Equal lengths of time, from 2½ to 3 hours, were spent at each station. In order to obtain a representative sample from each station, each type of nesting site was worked for a period of time proportionate to its abundance in that particular station. For example, in longleaf pine flatwoods there is more opportunity for ants to nest in the bases of trees than in the open sand, and therefore the former was collected proportionately longer than the latter in that association.

Most of the collections were made with forceps, and some were made with an aspirator. The daily collection from each station was supplemented by putting the litter from approximately two square feet of soil surface through a Berlese funnel. The litter was left on the funnel with no external heat for two or three days until dry.

To sample the contents of the litter in the field, several other Berlese-type funnels were built from five-gallon lard cans. The funnel itself consisted of an inverted light reflector which led to a hole in the bottom of the can; over the light reflector different mesh screening or hardware cloth could be placed. To activate the animals a few drops of household ammonia were introduced, and the top placed on the can. Such funnels were left an hour or less.

Another supplementary Berlese-type funnel was made from a household funnel by fastening wire screen over its top and running a rubber tube from its bottom into a vial. Small pieces of wood, pieces of moss, and other similar objects were placed on this funnel, and a light bulb, usually sixty watts, was lowered in a reflector over the funnel. Other special collecting was accomplished by use of molasses traps, and a light trap. The ants from these last two funnels, and from the traps were not figured in the relative abundance.

For each colony collected, the blanks on a field data sheet were filled in, except when two or more collections of the same form were made in identical situations. In these cases, only one field data sheet was filled in, but the appropriate relative abundance was checked.

RELATIVE ABUNDANCE

If on one collecting trip of two and one-half hours to a given station an ant form was collected six times or more, it was considered abundant; if collected four or five times, common; two or three times, occasional; and if collected only once, it was treated as rare in that locality. The relative abundance data for each collecting trip was recorded in the field.

A form collected only once or twice in a given day may have a sporadic occurrence in the area of the station collected, and yet have a relatively high

abundance over a period of time in that station. Because of such possible discrepancies, a relative abundance figure based on the 17 collecting trips was compiled for each form in each station so as to give a truer representation. On this basis, a form is considered abundant if it was collected in a station forty times or more; common, if collected thirteen to thirty-nine times; occasional, if collected two to twelve times; and rare if collected once.

Collecting Stations on the Reserve

SUMMARY OF RECOGNIZED STATIONS

For convenience in referring to the field data sheet, the plant association-soil type combinations, or stations, are expressed by letters and numbers representing the drainage, vegetation, and soil type of the station. For example, IIa represents a well drained station supporting the *Pinus palustris-Quercus laevis* association on Lakeland fine sand. The stations chosen are:

I. Well drained areas other than hammocks
   1. *Pinus palustris-Quercus laevis* association
      a. Lakeland fine sand (Turkey oak sandhills or uplands)
   2. *P. palustris-Q. cinerea* association
      a. Blanton fine sand (Bluejack oak sandhills)
   3. *P. clausa-Q. virginiana* var. *geminata-Q. myrtifolia-Q. chapmanii* association
      a. St. Lucie fine sand (St. Lucie scrub or scrub)
   4. *Q. virginiana* var. *geminata-Q. myrtifolia-Q. chapmanii* association
      b. Leon fine sand, light colored surface phase (Leon scrubby flatwoods)
      d. Pomello fine sand (Pomello scrubby flatwoods)

II. Poorly drained flatwoods
   1. *P. palustris-Aristida stricta* association
      a. Leon fine sand (Longleaf pine flatwoods)
   2. *P. elliotti* association
      a. Plummer fine sand (Plummer slash pine flatwoods)
      b. Rutlege fine sand (Rutlege slash pine flatwoods)
   3. *P. serotina-Desmothamnus* association
      a. Plummer fine sand (Black pine-fetterbush flatwoods)

III. Hammocks (Well drained to nearly saturated)
   1. *Q. virginiana* association
      a. Blanton fine sand, hammock phase (Xeric hammock)
   2. *Magnolia grandiflora-Ilex opaca* association
      a. Blanton fine sand, hammock phase (Mesic hammock)
   3. *Q. nigra-Liquidambar-Sabal palmetto* association
      a. Rutlege fine sand (Hydric hammock)

IV. Seasonally flooded areas
   1. *Taxodium distichum-Nyssa biflora* association
      a. Peaty muck (River swamp)
   2. *Gordonia-Tamala pubescens-Magnolia virginiana* association
      a. Rutlege fine sand (Bayhead)
   3. *Mariscus jamaicensis* association
      a. Peaty muck (Marsh)

DESCRIPTIONS OF THE STATIONS[3]

TURKEY OAK SANDHILLS

The location of this station (fig. 4) is in the northeast portion of the Reserve, between Trails 10, 11, and 12. Characteristic trees are the longleaf pine (*P. palustris*[4]) and turkey oak (*Quercus laevis*). Bluejack oak (*Q. cinerea*) and live oak (*Q. virginiana*) are also present, but are not so plentiful. Below the widely spaced trees is a scanty herbaceous vegetation consisting in the main of wiregrasses (*Aristida stricta* and *Sporobolis gracilis*). Between these rather dense patches of wiregrass there are areas of bare, pale gray sand.

Lakeland fine sand (Laessle's Norfolk fine sand, deep phase) may occur on level or gently sloping areas of uplands, but on the Reserve it appears chiefly in the rolling turkey oak sandhills. The soil has good drainage, but it is not as excessive as that of St. Lucie fine sand and Lakewood fine sand. It has more organic matter in the surface layer than either of the latter soils.

BLUEJACK OAK SANDHILLS

This station is located at the junction of Trails 9 and 13 in the middle of the eastern side of the Reserve. The vegetation is similar to that of the turkey oak sandhills, except that bluejack oak (*Q. cinerea*) is the codominant instead of turkey oak. The pines of this station are larger and more numerous in a given area than in the turkey oak sandhills, and there is consequently more pine needle litter. This litter, along with the wiregrass and the litter added by the oaks, forms a complete and sometimes dense mat.

Blanton fine sand possesses good to fair drainage. Although the soil has no organic hardpan, there is a tendency toward one at depth of three feet where the soil borders Leon fine sand.

ST. LUCIE SCRUB

The area chosen for this station is located just over the Reserve fence at the end of Trail 13. Part of this area of scrub extends onto the Reserve east of Trail 13, but the larger area over the fence was chosen as more typical.

Laessle points out that the patch of scrub in question lacks certain characteristic plants of the Florida scrub in general. Important among these are rosemary (*Ceratiola ericoides*) and the semaphore cactus (*Opuntia austrina*). A rather dense growth of sand pine (*P. clausa*) makes up the upper story of the station, while scrub oaks, along with several other shrubs, comprise a lower layer. Among the oaks may be listed twin live oak (*Q. virginiana* var. *geminata*) and Chapman's oak (*Q. chapmanii*) while staggerbush (*Xolisma ferruginea*), saw palmetto (*Serenoa repens*), silk bay (*Tamala humilis*), and species of *Ilex* are other shrubs found at the station. A few vines and herbs, along with mosses and lichens are also to be found. It is pointed out by Laessle (1942) that "in spite of the xeromorphic nature of the scrub vegetation, with its small, heavily cutinized, often revolute, and hairy leaves

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[3] For a fuller discussion of the vegetation and soils of the Reserve as a whole, and of the stations mentioned here, the reader should see Laessle (1942).

[4] The scientific names of pines are taken from West and Arnold (1946).

. . . comparatively mesic conditions are found . . ." in scrub because of the close, low, and consequently dense growth.

St. Lucie fine sand is characteristic of higher areas where drainage is excessive or nearly so. Organic matter has opportunity to remain only in the

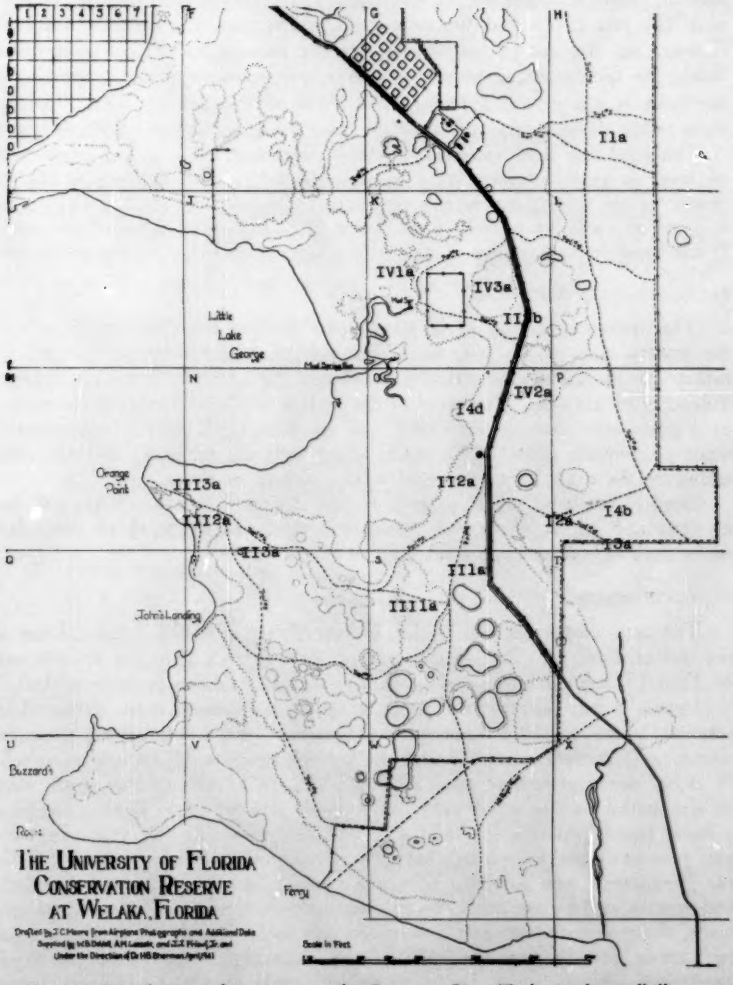


Fig. 4.—Distribution of stations on the Reserve. I1a—Turkey oak sandhills or uplands; I2a—Bluejack oak sandhills; I3a—St. Lucie scrub or scrub; I4b—Leon scrubby flatwoods; I4d—Pomello scrubby flatwoods; II1a—Longleaf pine flatwoods; II2a—Plummer slash pine flatwoods; II2b—Rutlege slash pine flatwoods; II3a—Black pine-fetterbush flatwoods; III1a—Xeric hammock; III2a—Mesic hammock; III3a—Hydric hammock; IV1a—River swamp; IV2a—Bayhead; IV3—Marsh.

first inch of the profile. Below this the rainwater leaches it rapidly through the large particles of what perhaps were ancient sand dunes, to give a loose, white sand.

LEON SCRUBBY FLATWOODS

This station is located between Trails 9 and 13 in the middle portion of the eastern side of the Reserve. The vegetation is like that of the St. Lucie scrub, except that the sand pine and the silk bay, as well as certain other plants, are absent. A few trees of longleaf pine are present as relics.

Leon fine sand, light colored surface phase (Laessle's Leon fine sand, scrubby phase) holds a position between Pomello fine sand and St. Lucie fine sand on the one hand, and the typical Leon fine sand on the other. It is better drained than the latter and more poorly drained than the former. The hardpan is usually within thirty to forty-two inches of the light gray or almost white surface.

POMELLO SCRUBBY FLATWOODS

The patch of this scrubby flatwoods studied is located one hundred yards west of the highway, and about 1/4 mile northwest of the fire tower. The vegetation is very much like that of the Leon scrubby flatwoods. Laessle (1942) sums up the differences between the two as follows: "I am able to detect no fundamental vegetational difference . . . except that there is a noticeable difference in the greater height attained by the shrubs of the Pomello soil and the longleaf pine always seems lacking there."

Pomello fine sand (Laessle's St. Lucie fine sand, flat phase) is more poorly drained than St. Lucie fine sand, and better drained than Leon fine sand. It differs from Leon fine sand, light colored surface phase, in drainage as noted above, and in possessing no hardpan within forty-two inches of the surface.

LONGLEAF PINE FLATWOODS

This station is located between Trail 4 and the highway, about 3/8 mile from the fire tower. The vegetation is dominated by somewhat scattered, large longleaf pines; small longleaf pines are quite abundant. Saw palmetto, gallberry (*Ilex glabra*), and fetterbush (*Desmothamnus lucidus*), as well as other shrubs, are found here. The ground cover consists largely of wiregrass (*A. stricta*), but much indian grass (*Sorghastrum secundum*) is present. Since fire has been kept out for several years now, the shrubs, especially those mentioned above, are growing profusely, and wiregrass is being forced out.

These flatwoods, which are fire subclimax for this region, grow on Leon fine sand. It is higher than Plummer fine sand and Rutlege fine sand. Leon fine sand has a gray or salt-and-pepper surface becoming lighter down to a brownish black hardpan consisting of fine sand particles cemented together with organic matter. Below the hardpan, which is at twenty-eight to thirty-four inches from the surface, the sand is only partially cemented with organic matter, and becomes lighter brown with depth.

PLUMMER SLASH PINE FLATWOODS

The location of this station is a little less than 1/4 mile southwest of the

fire tower. It supports the dominant slash pine (*P. elliotti*) and a few longleaf and black pines. Saw palmetto and other shrubs are present, along with several grasses, among them *Andropogon*.

Plummer fine sand, found in many cases between longleaf pine flatwoods and the lower hydric hammocks, is a gray to light gray soil. It contains a brown stained fine sand, usually at about three feet.

RUTLEGE SLASH PINE FLATWOODS

This station is north of Trail 3 and just west of the highway. The vegetation, dominated by slash pine (*P. elliotti*), and composed of scattered trees of longleaf pine (*P. palustris*) and black pine (*P. serotina*), is similar to that of Plummer slash pine flatwoods. Its shrubs consist of fetterbush (*Desmothamnus lucidus*), saw palmetto (*Serenoa repens*), and others. Because of lack of fire, these shrubs have become dense, and are in many places shading out the ground layer of short grasses.

The surface ten inches of Rutlege fine sand (Laessle's Portsmouth fine sand) contain much organic matter and are dark gray or black. The station is low, and in times of heavy rain the soil may become supersaturated.

BLACK PINE-FETTERBUSH FLATWOODS

This station is about 1/4 mile east of the junction of Trails 6 and 8, on the south side of Trail 6, near the middle of the west side of the Reserve. The trees of the area are widely scattered black pine (*P. serotina*), but thickets of fetterbush are fairly dense between the pines. Among these thickets are open areas with little or no litter in which the most important plants are broom sedge (*Andropogon*) and shorter grasses. The thickets themselves are on areas raised a few inches above the lower, open soil, presenting available space for nests when the lower areas become temporarily supersaturated during the summer rains.

Although the soil of this station (designated St. Johns fine sand by Laessle) may not be typical Plummer fine sand, it is placed under that heading. The lack of a hardpan within the eighteen to twenty-four inch level suggests Plummer rather than the best alternative, St. Johns fine sand. Over the surface of the very flat area, the organic matter is tightly packed.

XERIC HAMMOCK

Located in the only large area of live oak on the Reserve, this station extends between Trails 6 and 7 from near their junction for about a quarter of a mile. The dominant tree is live oak (*Q. virginiana*). There are also numbers of bluejack oak (*Q. cinerea*) and laurel oak (*Q. laurifolia*), and some cabbage palmetto (*Sabal palmetto*). A few trees of longleaf pine (*P. palustris*) and loblolly pine (*P. taeda*) are present. Chapman's oak, as well as other shrubs, wild grapes (*Vitis* spp.), virginia creeper (*Parthenocissus quinquefolia*), and grasses of the genus *Panicum* make up part of the rest of the flora. Because of the well-spaced large trees, the area is quite open, except in those clumps where scrub oaks, with other lower vegetation, have grown together to form more or less dense thickets.

Blanton fine sand, hammock phase, has a profile much like that of the

typical Blanton fine sand. The soil at this station is higher than that of the surrounding Leon fine sand flatwoods.

MESIC HAMMOCK

This station is next to the river, just south of Orange Point. The area supports a denser growth than the xeric hammock. The top canopy allows comparatively little sunlight to filter through, and consequently the litter is moist much of the time. While it is not mature enough to represent a typical climax association, it does support bull bay (*Magnolia grandiflora*) and American holly (*Ilex opaca*), along with various large oaks and pignut hickory (*Hicoria glabra*). Saw palmetto and staggerbush (*Xolisma ferruginea*) are abundant. Among the vines are scuppernong (*Muscadina rotundifolia*), *Smilax bonanox,* and virginia creeper. Few herbs are present. As in the xeric hammock, the soil type here is Blanton fine sand, hammock phase.

HYDRIC HAMMOCK

The site of this station is 1/8 mile west of the junction of Trails 6 and 8 at Orange Point, between the mesic hammock just described and the lower river swamp. Water oak (*Q. nigra*), sweetgum (*Liquidambar styraciflua*), and cabbage palmetto (*Sabal palmetto*) are common. Also prevalent are swamp red bay (*Tamala pubescens*) and Florida elm (*Ulmus floridana*). Large relic slash pines are also to be found infrequently. Poison ivy (*Toxicodendron radicans*) and blaspheme vine (*Smilax laurifolia*), and the shrubs wax myrtle (*Cerothamnus ceriferus*) and saw palmetto are not uncommon. In a lower layer, *Osmunda* spp. are to be found. The ground, which at times becomes very wet to saturated, supports patches of sphagnum. The Rutlege fine sand is much the same as described under Rutlege slash pine flatwoods. It supports a comparatively dense growth, the top canopy of which is broken in only a few places.

RIVER SWAMP

This station is located just north of Mud Springs. Dominant among the trees which form a fairly thick canopy are bald cypress (*Taxodium distichum*), water tupelo (*Nyssa biflora*), red maple (*Rufacer rubrum*), and cabbage palmetto. The shrubs buttonbush (*Cephalanthus occidentalis*), *Salix longipes,* and wax myrtle are present, along with several vines, and only few herbs. The peaty muck is high in organic material from the decomposition of debris, and is consequently dark brown or black. There is standing water at this station almost all year, except just before the summer rainy season. The water isolates hummocks, formed by the root systems of trees and raised a foot or more above the lowest level of the ground.

BAYHEAD

The bayhead used for this station is about 1/4 mile south of the gate to Trail 3 on the east of the highway. Dominant in this station are the broad-leaved evergreens, loblolly bay (*Gordonia lasianthus*), swamp red bay (*Tamala pubescens*), and white bay (*Magnolia virginiana*). A few shrubs, chiefly wax myrtle, are supported, as well as blaspheme vine and poison ivy. The dense canopy allows little herbaceous growth, but sphagnum patches occur. This

bayhead is formed in a depression of the longleaf pine flatwoods which surrounds it. As its name suggests, bayheads head up incipient streams which find their way to the river, and consequently maintain standing water at almost all seasons, except perhaps just before the summer rainy season. Certain portions, especially toward the edge, remain comparatively dry, but the Rutlege fine sand is always moist.

MARSH

The area of this station is between Trails 2 and 3, near Mud Springs. It supports a growth of dominant sawgrass (*Mariscus jamaicensis*), scattered buttonbush, and *Sagittaria,* along with several other smaller plants. The saw grass is in most parts of the station so thick that not much, if any, plant life exists besides the saw grass.

The peaty muck of this station is covered with water almost all year. A foot or a foot and one-half of water accumulates during the summer rainy season. Unlike the river swamp, the ground here is completely covered with water, and there are no saturated, emergent hummocks.

Ecological Relationships

By means of repeated collecting trips to the stations, it was found that each contained a characteristic and distinctive assemblage of ant forms. The stations therefore represent ant habitats. It was also discovered that certain strata and nesting sites contained distinctive assemblages. These could also then be considered ant habitats.

DESCRIPTION OF THE STRATA AND NESTING SITES

The strata found to be significant in designating assemblages in the present study are 1) subsurface or subterranean, 2) surface or ground, 3) grass or herbaceous, and 4) shrub or arboreal. Included in the first stratum are all those nests which occur in sand, whether they are under logs, litter, or some other cover, or are in the open with no cover. Nests in the surface stratum are those which occur in any of the following: litter, fallen log, palmetto root on ground, under mat of palmetto root or trunk, dead stump, base of living tree, and grass clump. Those nests which are built in and under logs are included in the stratum in which their largest portions were found. For example, if a colony has its largest part in a log rather than in the sand under the log, the nest is recorded in the surface stratum. The herbaceous stratum consists of two nesting sites, namely, in tall grass stems (includes *Mariscus*), and in and between sawgrass blades. The shrub or arboreal stratum includes small branches, twigs, or galls.

SUBTERRANEAN STRATUM

Open sand.—Those nests which were found in sand with no cover. These were divided into four types: 1) no crater—any nest built in the open with no crater of sand pellets on the surface around the nest opening; 2) rudimentary crater—those nests in which a mound or string of several or many openings was built in seemingly unorganized fashion; 3) incomplete crater—

those nests in which the crater of sand pellets was not built in a complete circle; and 4) complete crater—a nest with a complete circle of sand pellets around the nest opening. Incomplete craters are probably only unfinished complete craters.

In and under litter.—Indicates situations in which a nest may be either in and under litter or merely under litter. Most of the nests in this category were actually under litter. A majority of the nests which extended from the sand into litter were probably only in litter temporarily.

Under log.—Those nests in sand with the nest openings under logs.

Under and in log.—Those nests with portions of the colonies both under logs and in logs.

SURFACE STRATUM

In fallen logs.—Includes all logs except those of palmetto.

Palmetto logs on ground.—With their scaly structure, offered a distinct nesting site, which even though rarely found was usually inhabited.

In living palmetto root or trunk.—On living palmetto roots and on the bases of palmetto trunks, nests occur in the debris beneath the mat and between the bases left by fallen fronds.

In dead stumps, and in the bark at the bases of living trees.—Usually occurred in the moist first four inches above the soil surface.

In litter.—Those nests built in and on fallen leaves, especially live oak. This type of nest occurred most often in mesic hammock on oak leaves which had fallen so that the convex surface was next to the ground. The ants lived on the inverted, concave surface, and the colony was covered by one or more leaves. This was a favorite nesting site of *Paratrechina parvula* (Mayr), and although other ants, such as *Pheidole dentata* Mayr, were found in it, they nested there only seldom. Other nests in this category were taken in the lower areas of the Reserve from piles of pine needles supported by low vegetation.

In the bases of grass clumps.—Built mostly between the appressed blades of grass and in the roots. Various ants occur in this nesting site, usually in low areas such as Rutlege slash pine flatwoods, but again *Paratrechina parvula* (Mayr) is most abundant. Nests of this kind are especially numerous during the wet season. Although this category was first placed in the herbaceous stratum, its close relation to other nesting sites in the surface stratum makes it necessary to place it in the latter stratum.

HERBACEOUS STRATUM

Between sawgrass blades.—This category is very much like the last in that the ants nest between appressed blades. Where sawgrass occurs, however, there is standing water most of the year, and nests cannot extend into the roots. *Paratrechina parvula* (Mayr) is a major inhabitant of the sawgrass too.

Tall grass stems.—Most of the tall grass in which ants live is of the genus *Andropogon*. Other tall grasses do not allow enough room for the ant to

move within the stem. One of the few inhabitants of the tall grass stem is *Pseudomyrma pallida* F. Smith, but it is found there abundantly. Also included within this category are the flower stalks of sawgrass, although the occurrence of ants within them is not great.

ARBOREAL STRATUM

Twigs.—Those branches from which the center core of wood is absent, providing only enough room for the ant to crawl through.

Small branches.—Those branches which have multiple passageways, or which retain only the bark and a very little of the wood.

Galls.—Nests in galls seem to be made only after the gall insect has emerged. The ants always use the opening made by the emerging gall insect as a nest opening, but some galls showed additional openings quite evidently made by the ants.

A miscellaneous category, "other", is used for nests in pine cones, fern roots, under stones, and other such places which are of little consequence for nesting on the Reserve.

AVAILABILITY OF NESTING SITES IN STATIONS

Table I shows the relative abundance of places to nest in the various stations. This abundance is purely subjective, based on the field experience of the author, and is used to indicate the abundance of a given place to nest in a given station relative to that of the same place in another station. The column "Litter" serves a double purpose in designating the availability of nesting places both in litter and in and under litter. Likewise, the column "Broadleaved or pine logs" indicates the availability of places to nest in and under logs, under logs, and in fallen logs. The table therefore indicates the availability of the nesting sites in the stations.

In parts of hydric hammock and bayhead, litter not only covers the whole surface area, but it is also thick, sometimes reaching a depth of six inches or more. Ants that lived under litter were found to be at a minimum, being replaced by ants living in litter and in the maze of roots and decaying logs buried in litter. Litter is common or abundant in almost every station except swamp and marsh. Here the availability of nesting sites in litter is cut down by the seasonally standing water. In stations such as xeric hammock and turkey oak, where the tree, shrub, and herb growth is widely spaced, large patches of bare sand are present.

Logs are not abundant on the Reserve, except in hydric hammock and river swamp, because of the logging operations being carried on. In the swamp, however, most of the logs are under water most of the year, and consequently offer no nesting places. The column "Living trees and shrubs" indicates the abundance of the possible nesting places in the bases of trees and shrubs. Nesting sites are found almost always in the bases of pine trees, rather than in the bases of broadleaved trees.

"Grass clumps" shows the abundance of clumps of grass, including the bases of the tall grasses. "Tall grass plants" denotes *Andropogon*. The stems, in which the ants live, die in the winter, and although some remain

TABLE 1.—Availability of nesting sites.

				Flatwoods						Hammock					
	Turkey oak	Bluejack oak	Scrub	Leon	Pomello	Longleaf	Plummer	Rutlege	Black pine	Xeric	Mesic	Hydric	River swamp	Bayhead	Marsh
Sand with no litter	O-C	R-O	R-O	O	O	R	R	–	R	C	R	–	–	–	–
Litter	C	A	A	C	C-A	A	A	A	C-A	O-C	A	A	R-O	A	–
Broadleaved or pine logs	O	C	C	R	R	O	O	R	R	O-C	O	C	A	C	–
Palmetto logs	–	–	R	R	R	R	R	R	R	–	R	R	–	–	–
Palmettos	–	–	C	C	C	C	C	C	C	R	A	O	R	R	–
Broadleaved or pine stumps	O-C	C	R	R	R	O	R	R	R	O	O	C	O	R	–
Living trees and shrubs	C	C	A	A	A	C	C	O	O	C	A	A	A	A	R
Grass clumps	–	R	R	R	R	R-O	C	A	C	O	R	R	–	–	–
Sawgrass plants	–	–	–	–	–	–	–	–	–	–	–	–	–	–	A
Tall grass plants	–	–	–	–	–	C	O	R	A	R	–	–	–	–	–
Twigs	R	R	O	O-C	R-O	R	R	R	–	O	C	C	C	O	C
Small branches	C	C	O-C	A	A	O	O	R	R	O	A	A	C	C	–
Galls	R	O	O	C-A	A	–	–	–	–	O	R	–	–	–	–

R—rare; O—occasional; C—common; A—abundant.

TABLE 2.—Relative abundance of ant forms in stations.

	Turkey oak	Bluejack oak	Scrub	Flatwoods: Leon	Pomello	Longleaf	Plummer	Rutlege	Black pine	Hammock: Xeric	Mesic	Hydric	River swamp	Bayhead	Marsh
1. Eciton nigrescens	–	–	–	–	–	–	–	–	–	–	R	–	–	–	–
2. E. opacithorax	–	–	–	–	–	O	–	–	–	–	–	–	–	–	–
3. Amblyopone pallipes	–	–	–	–	–	–	–	–	–	–	–	–	–	R	–
4. Proceratium croceum	–	R	–	–	–	O	–	–	–	–	–	–	–	–	–
5. Pr., near silaceum	–	–	–	–	–	–	R	–	–	–	–	–	–	–	–
6. Euponera gilva	–	–	–	–	–	–	–	–	–	–	R	O	–	–	–
7. Ponera ergatandria	R	R	–	–	–	–	–	–	R	–	O	O	–	–	–
8. P. opaciceps	–	–	–	–	–	–	–	R	–	R	–	C	C	R	A
9. P. trigona opacior	O	O	O	O	–	R	O	R	R	C	O	O	–	O	–
10. Leptogenys elongata manni	–	–	–	–	–	–	–	–	–	–	–	–	R	–	–
11. Odontomachus haematoda insularis	C	O	O	C	O	C	C	O	A	C	A	C	C	C	–
12. Pseudomyrma brunnea	O	–	R	O	O	–	–	R	–	R	O	O	O	R	O
13. Ps. pallida	O	O	–	C	–	C	O	O	A	R	–	–	–	–	–
14. Pogonomyrmex badius	O	O	–	–	–	–	–	–	–	C	–	–	–	–	–
15. Aphaenogaster ashmeadi	R	O	O	O	–	–	–	–	–	C	O	–	–	R	–
16. A. floridana	O	–	–	–	–	–	–	–	–	–	–	–	–	–	–
17. A. fulva	–	–	O	–	–	O	–	R	–	R	–	O	C	O	R
18. A. lamellidens	–	–	–	–	–	–	–	–	–	R	–	–	–	–	–
19. A. macrospina	–	O	–	–	–	O	–	O	–	–	–	–	–	–	–
20. A. texana	–	–	O	–	–	R	–	–	–	R	R	–	–	–	–
21. A. treatae	–	–	R	O	–	–	–	–	–	–	–	–	–	–	–
22. Pheidole dentata	C	A	A	A	A	C	C	C	C	C	A	C	A	O	R
23. Ph. dentigula	–	–	O	–	O	–	O	?	–	O	O	O	–	O	–
24. Ph., near floridana	C	C	R	R	C	O	O	O	R	R	O	R	O(?)	–	–
25. Ph. metallescens	C	C	C	C	–	R	–	–	–	A	O	–	–	–	–

R—rare; O—occasional; C—common; A—abundant.

TABLE 2.—(*continued*)

	Turkey oak	Bluejack oak	Scrub	Flatwoods: Leon	Pomello	Longleaf	Plummer	Rutlege	Black pine	Hammock: Xeric	Mesic	Hydric	River swamp	Bayhead	Marsh
26. Ph. morrisi	O	O	–	O	O	–	–	–	–	C	–	–	–	–	–
27. Ph. pilifera	Orange grove														
28. Cardiocondyla emeryi	–	R	–	–	–	–	–	–	–	O	–	–	–	–	–
29. Car. nuda minutior	–	–	–	–	–	R	–	–	–	?	–	–	–	?	–
30. Car. wroughtoni bimaculata	C	–	–	R	–	R	–	–	–	–	–	–	–	–	–
31. Crematogaster minutissima missouriensis	–	O	O	–	R	–	C	O	–	O	C	C	R	C	–
32. Cr. ashmeadi	O	O	C	C	A	C	R	–	R	O	O	R	O	–	–
33. Cr. coarctata vermiculata	–	–	–	–	–	–	–	–	–	–	–	O	O	–	–
34. Cr. clara	R	O	–	–	–	C	C	A	–	R	O	C	–	C	A
35. Cr. lineolata	–	–	–	O	C	–	–	–	–	O	–	–	–	–	–
36. Monomorium floricola	R	–	–	–	–	–	–	–	–	–	–	–	–	–	–
37. M. minimum	O	–	–	–	–	–	–	–	–	–	–	–	–	–	–
38. Solenopsis geminata	O	O	R	C	O	O	–	–	–	O	–	O	O	–	–
39. S. rufa	R	–	–	–	–	R	O	–	–	–	–	–	–	–	–
40. S. globularia littoralis	–	–	–	–	–	–	–	–	O	–	–	–	–	–	–
41. S. minutissima ?	O	O	O	–	O	–	O	–	–	R	O	O	R	O	–
42. S. molesta	O	O	C	O	O	O	C	O	O	O	A	C	–	O	–
43. S. pergandei	O	–	–	R	–	–	–	–	–	O	R	–	–	–	–
44. S. picta	O	O	O	O	O	O	O	O	R	R	O	O	R	C	–
45. Myrmecina americana	–	–	R	–	–	–	–	–	–	–	–	–	–	–	–
46. Leptothorax pergandei floridanus	C	C	C	C	O	C	R	–	C	C	O	R	–	–	–
47. L. texanus davisi	O	R	–	O	–	–	–	–	R	R	–	–	–	–	–
48. Tetramorium guineense	R	–	–	–	–	–	–	–	–	–	–	O	?	–	O
49. Strumigenys louisianae	R	R	–	–	–	–	–	–	–	R	R	–	?	–	–
50. Smithistruma bunki	R	–	–	–	–	–	–	–	–	–	–	–	–	–	–

TABLE 2.—(*continued*)

	Turkey oak	Bluejack oak	Scrub	Flatwoods: Leon	Pomello	Longleaf	Plummer	Rutlege	Black pine	Hammock: Xeric	Mesic	Hydric	River swamp	Bayhead	Marsh
51. Sm. clypeata	–	–	–	–	–	–	–	–	–	O	–	–	–	–	–
52. Sm. creightoni	–	–	–	–	–	–	–	–	–	O	–	–	–	R	–
53. Sm. dietrichi	O	R	–	–	–	–	–	–	–	–	–	–	–	–	–
54. Sm. ornata	–	–	R	–	–	–	–	–	–	–	R	–	–	–	–
55. Sm. pulchella	–	–	–	–	–	–	–	–	–	R	–	–	R	–	–
56. Sm. talpa	–	–	–	–	R	–	–	–	–	–	R	R	–	R	–
57. Trachymyrmex septentrionalis seminole	C	O	O	O	O	–	–	–	–	C	R	–	–	–	–
58. Dolichoderus pustulatus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	O
59. Iridomyrmex humilis	Palatka, ruderal														
60. I. pruinosus	C	O	O	O	O	C	–	–	C	O	–	–	–	–	–
61. Dorymyrmex pyramicus flavopectus	Welaka, ruderal														
62. D. pyramicus	O	R	–	–	–	–	–	–	–	O	–	–	–	–	–
63. Tapinoma sessile	–	–	–	–	–	–	–	–	–	–	–	–	–	–	R
64. Brachymyrmex depilis	O	O	O	O	O	C	C	O	C	–	O	O	–	O	–
65. Camponotus castaneus	–	–	O	O	O	R	R	O	–	O	O	R	O	O	–
66. C. socius	C	O	–	O	–	–	–	–	–	C	–	–	–	–	–
67. C. nearcticus	O	O	R	–	O	O	–	–	–	–	O	–	O	R	–
68. C. (Colobopsis) spp.	–	–	O	–	O	–	R	R	–	O	O	O	O	O	C
69. C. abdominalis floridanus	C	C	C	C	O	C	C	O	C	C	C	C	O	O	O
70. Paratrechina longicornis	Crescent City, ruderal														
71. Par. arenivaga	A	R	–	O	R	R	R	–	–	A	–	–	–	–	–
72. Par. parvula	C	O	O	C	O	C	C	C	A	C	A	C	O	C	A
73. Prenolepis imparis	R	–	O	–	–	–	–	–	–	–	–	–	–	–	–
74. Formica archboldi	O	–	–	–	–	O	O	R	O	R	–	–	–	–	–
75. F. pallidefulva	O	–	–	–	R	–	–	–	–	O	–	–	–	–	–
76. F. schaufussi	R	–	–	–	–	R	–	–	–	–	–	–	–	–	–

suitable for nesting sites throughout the year, there is a tendency for this nesting site to disappear seasonally.

DISTRIBUTION OF ANT FORMS IN STATIONS

Table 2 shows the distribution of ant forms in stations on the Reserve. In general, they preferred the higher and more open areas in which to nest. Xeric hammock and turkey oak contained the largest number of forms with 43 and 42 respectively. The next 11 stations held smaller and smaller numbers of forms, the numbers diminishing by one to three per station. The black pine-fetterbush flatwoods supported only 17 forms, and the number dropped to 11 in marsh. The number of forms per station is as follows: Xeric hammock—43; turkey oak—42; bluejack oak—33; scrub—30; mesic hammock—30; longleaf pine flatwoods—29; hydric hammock—27; Leon scrubby flatwoods—27; Pomello scrubby flatwoods—25; bayhead—24; Plummer slash pine flatwoods—22; river swamp—21; Rutlege slash pine flatwoods—20; black pine-fetterbush flatwoods—17; marsh—11. The mean number of forms collected in one station is 26.7, a figure lying between hydric hammock or Leon scrubby flatwoods and Pomello scrubby flatwoods, near the middle of the list.

The difference of 9 forms between the first two stations and the next highest probably indicates an aspect of the unnaturalness of the Reserve. Where there should be logs under what are natural conditions in other portions of the state, the timber has been removed on the Reserve before it fell. Longleaf pine flatwoods and mesic hammock should contain more fallen logs than they do, with a correspondingly greater number of log-inhabiting forms. In Gainesville, a more typical mesic hammock, with 39 forms, contained the highest number of ants collected in any plant association there.

Turkey oak and xeric hammock offer the greatest opportunity for nesting in open sand. They are therefore able to attract those ants which prefer or must have nesting sites in open areas. At the same time they offer dry or moist litter, a few logs, and arboreal sites.

Two factors should be mentioned in regard to longleaf pine flatwoods. First, the logging operations remove many logs which would provide nesting sites, and perhaps attract a greater number of species to the area. Second, fire is conscientiously kept out of the Reserve. As a consequence, there is a dense growth of shrubs in the flatwoods and litter is becoming deeper over the whole area.

Only 17 forms were taken from black pine-fetterbush flatwoods. Since the station offers very little diversity of nesting sites, it excludes most of the other ants found on the Reserve. During the summer months it has standing water after every heavy rain; this tends to limit the ants to those which can withstand periodic submergence.

The low number of forms in marsh can also be traced to the small number of available nesting sites in that plant association. For all but a few months of the year there is standing water. There are no trees, but only scattered shrubs to offer small branches and twigs. The great majority of the nesting sites are between the appressed blades of sawgrass.

The number of collections made (the number of nests collected) in each station is as follows: Turkey oak—425; xeric hammock—373; black pine-

fetterbush flatwoods—307; mesic hammock—295; Leon scrubby flatwoods—280; hydric hammock—245; scrub—226; bluejack oak—224; longleaf pine flatwoods—219; Pomello scrubby flatwoods—218; marsh—184; river swamp—167; Plummer slash pine flatwoods—166; bayhead—128; Rutlege slash pine flatwoods—120. The mean number of collections made in one station is 238.4, a figure lying between hydric hammock and scrub.

It will be noted that turkey oak and xeric hammock are at the top of the list with the greatest number of collections, as well as with the greatest number of forms. This emphasizes that these two stations are best suited to the ants for nesting situations. In the latter chart also, the higher and more open areas are at the top of the list. In this connection, the open black pine-fetterbush flatwoods was next to lowest in the number of forms taken from it, but it is third when the number of collections is considered. This indicates that black pine-fetterbush flatwoods is particularly favorable for the few ant forms occurring there. The opposite trend is shown by bluejack oak, which is relatively low in number of collections, but high in number of ant forms; such a trend indicates that suitable nesting sites are diverse, but scarce.

In general, those places in which the moisture and litter are intermediate are in the middle of the list. Last on the list are the seasonally flooded areas and the slash pine flatwoods. Marsh, which has the fewest number of forms, is more toward the middle of the list in numbers of collections. Bayhead and the slash pine flatwoods, on the other hand, are lower on the present list.

Since some of the stations differ in their positions on the lists more or less considerably, the number of forms per station and the number of collec-

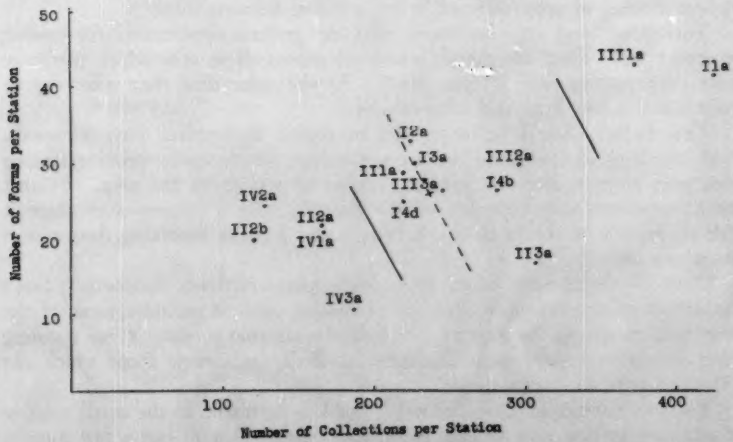


Fig. 5.—Suitability of the stations for ants, based on the number of ant forms per station weighted against the number of collections per station. I1a, turkey oak; I2a, bluejack oak; I3a, scrub; I4b, Leon scrubby flatwoods; I4d, Pomello scrubby flatwoods; III1a, longleaf pine flatwoods; II2a, Plummer slash pine flatwoods; II2b, Rutlege slash pine flatwoods; II3a, black pine flatwoods; III1a, xeric hammock; III2a, mesic hammock; III3a, hydric hammock; IV1a, river swamp; IV2a, bayhead; IV3a, marsh.

tions per station are weighted in fig. 5 to obtain the over-all suitability of each station as a nesting situation. The numbers and letters near each point on the graph indicate the station which that point represents. It will be noted that three major groups are shown, separated on the graph by the solid black lines. The group lowest in the number of species and the number of collections per station contains all of the seasonally flooded areas plus the slash pine flatwoods. Plummer slash pine flatwoods is higher than Rutlege slash pine flatwoods in number of species and in number of collections, bearing out its closer resemblance in the field to longleaf pine flatwoods.

The middle group contains mesic and hydric hammock, bluejack oak, scrub, and all of the flatwoods, including scrubby flatwoods. It is possible that the thick stand of pine in the bluejack oak area is responsible for its relation to the longleaf pine flatwoods on the graph. The last group, xeric hammock and turkey oak, is outstanding for the large number of species and collections made in its two stations.

The "x" in fig. 5 represents the point at which the mean number of collections per station intersects the mean number of forms per station. Those stations to the right of the dashed line are more suitable than average for ants, while those on the left are less suitable than average.

Plant succession as depicted by Laessle for the Reserve (1942) is shown in fig. 6. Three psammoseres recognized are 1) active dunes or strongly wave-washed sands, leading eventually to scrub, 2) residual sands neither strongly wind-sorted nor wave-sorted, with rolling topography, leading to the sandhills of turkey oak and bluejack oak, and 3) washed and sorted marine sands, with flat topography, leading to longleaf pine flatwoods. The hydroseres lead, on the one hand, through successive stages to bayhead, and on the other, through similar stages to marsh. The relationships of the black pine-fetterbush flatwoods are obscure, but it is possible that they originate in much the same way as the longleaf pine flatwoods, and that bayhead vegetation replaces the flatwoods, from the lower portions. The transition from hydric hammock to mesic hammock is also possible, but Laessle had not observed such a replacement on the Reserve. It will be noted that longleaf pine flatwoods may be replaced by either scrubby flatwoods or slash pine flatwoods, depending upon whether succession takes place in the higher or the lower portions. Laessle recognizes three fire subclimaxes: 1) scrub; 2) the sandhills; and 3) longleaf pine flatwoods. The climax is mesic hammock.

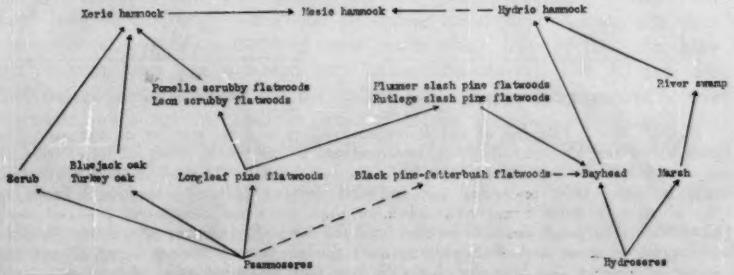


Fig. 6.—Plant succession on the Reserve. (After Laessle.)

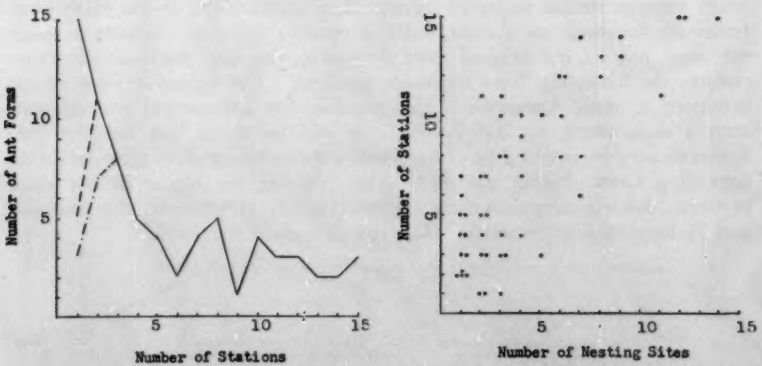
In general, those stations near each other in succession are found near each other on the graph (fig. 5). This situation is probably a reflection of the moisture conditions in the various associations. The groups on the graph could be called xeric, mesic, and hydric, with little overlap. The graph shows that the hydric situations have the least number of species and collections per station, while the xeric situations have the most.

Another important relation is plotted in fig. 7. The solid black line shows the number of ant forms occupying one station, the number occupying two stations, etc. The dashed line shows the number of forms per given number of stations for those forms collected more than once; and the line of dashes and dots, for those collected more than twice.

Note that only in the first case is there a large number of forms (about 21%) taken in one station. In the case of those ants which were collected more than once, only 5, or 8%, are confined to one station. Of those forms collected more than twice, only 3 ants, or about 5%, are limited to one station. As this procedure is continued, the number of ants in only one station tends to become smaller and will finally reach zero at eleven collections.

The dashed line graph has a peak where the number of stations equals two. In graphs excluding ant forms collected two times or less, three times or less, etc., the peak moves over to three stations. The cause of this peak is obscure, but it may indicate that the ants of the Reserve will, in most cases, be found to occupy at least three stations when enough collections are made.

It can be pointed out that the graphs do not dip strongly as the number of stations is increased. They tend toward a straight line at two to three forms for the higher number of stations.



Figs. 7, 8.—7. Number of ant forms confined to a given number of stations. The figure shows that 15 forms, or 21%, were confined to one station when all forms collected are considered (——) (N = 72). This number drops to 5 forms, or 8%, when those forms collected only once are not included (– – –) (N=62), and to 3 forms, or 5%, when only those forms collected more than twice are considered (— . — . —) (N = 56). The graph tends to become level for the higher number of stations. 8. Scatter diagram to show the relationship between the number of stations occupied and the number of nesting sites occupied for each ant form collected more than three times. (N = 52.)

The 21% of the ant forms taken in only one station is comparable to the 20% of the ant forms of the Chicago region that Talbot (1934) took in one plant association. Likewise, Gregg (1944) showed about 24% of the ant forms of the same region confined to one plant association, but Cole (1940), in the Great Smoky Mountains, found about 48% of the ants confined to one plant association. His high percentage may in part have been caused by the differing altitudinal levels of his plant associations.

Neither Talbot nor Cole mentions the number of times each ant form was collected. Even though Gregg gives relative abundance figures for each species, these apply to the whole area worked, rather than to his plant associations. On the basis of the figures he presents, however, none of the ants collected in only one plant association was common or abundant. When his ants were found to be common or abundant they were always collected in more than one plant association. This also holds true for the Reserve. Only those collected rarely or occasionally were confined to one station. This fact makes it plausible to suggest that in their distribution, perhaps with the exception of the mountainous areas, ants do not show as much dependence upon stations based on plant associations as other animals.

It is interesting to note that only three of the forms listed by Talbot as confined to one plant association were found in but one plant association by Gregg ten years later. In view of this fact and in consideration of the observations made during the present study, it becomes quite clear that even after a thorough investigation of a given area has been completed, continued collecting in that area will increase the number of stations in which certain of the ants are found. This can also be used in support of the contention that ants are not as restricted by factors in plant association-soil type combinations as are other animals.

DISTRIBUTION IN THE STRATA AND NESTING SITES

The ant forms collected on or near the Reserve were found to have the following distribution as to strata: Subterranean stratum—38; surface stratum —38; herbaceous stratum—11; arboreal stratum—16. The subterranean and surface strata contained a majority of the ant forms on the Reserve with a total of 58 in the two. Only 19 forms nested in the herbaceous and arboreal strata.

Table 3 shows this relationship. Of the total of 75 ants, 1 form was found only in buildings, while for 10 others no definite nesting site data were gathered. A few collections were made which may or may not have been colonies; they are indicated with a question mark. The 10 ants for which no data were obtained and the ruderal form, along with the questionable collections, were not included in arriving at the distributional data. The number of ants concerned was therefore 64. A single "x" indicates that the form was collected too few times for a preference to be recognized in table 3.

Distribution according to nesting sites was as follows:

Subterranean stratum.—Open sand—21 (no craters—12, rudimentary craters—7, incomplete craters—6, complete craters—13); under logs—10; in and/or under litter—31. There were 34 forms which lived under cover of either logs or litter. Nests of 9 forms were found under and in logs.

TABLE 3.—Distribution of ant forms in strata.
*—found only in one stratum; P—preferred stratum; x—additional strata; N = 64.

Species	Subterranean	Surface	Herbaceous	Arboreal
1. Eciton nigrescens	x	?	–	–
2. E. opacithorax	x	?	–	–
3. Amblyopone pallipes	–	x	–	–
4. Proceratium croceum	–	*	–	–
5. Pr., near silaceum	–	x	–	–
6. Euponera gilva	–	*	–	–
7. Ponera ergatandria	–	x	–	–
8. P. opaciceps	–	P	x	–
9. P. trigona opacior	x	P	–	–
10. Odontomachus haematoda insularis	P	x	–	–
11. Pseudomyrma brunnea	–	–	x	P
12. Ps. pallida	–	–	P	x
13. Pogonomyrmex badius	*	–	–	–
14. Aphaenogaster ashmeadi	*	*	–	–
15. A. floridana	*	–	–	–
16. A. fulva	x	P	–	–
17. A. lamellidens	–	–	–	x
18. A. macrospina	*	–	–	–
19. A. texana	–	*	–	–
20. A. treatae	*	–	–	–
21. Pheidole dentata	x	P	–	x
22. Ph. dentigula	x	P	–	–
23. Ph., near floridana	x	P	–	–
24. Ph. metallescens	P	x	–	–
25. Ph. morrisi	*	–	–	–
26. Ph. pilifera	*	–	–	–
27. Cardiocondyla emeryi	?	–	–	–
28. Car. nuda minutior	–	X	–	–
29. Car. wroughtoni bimaculata	–	P	x	–
30. Crematogaster minutissima missouriensis	x	P	–	x
31. Cr. ashmeadi	–	x	–	P
32. Cr. coarctata vermiculata	–	–	–	*
33. Cr. clara	–	x	x	P
34. Cr. lineolata	x	P	–	x
35. Monomorium floricola	–	–	–	?
36. M. minimum	*	–	–	–
37. Solenopsis geminata	P	x	–	–
38. S. rufa	P	x	–	–
39. S. globularia littoralis	–	*	–	–
40. S. minutissima ?	–	*	–	–
41. S. molesta	x	P	–	–
42. S. pergandei	P	x	–	–
43. S. picta	?	x	–	P

TABLE 3.—(*continued*).

Species	Subterranean	Surface	Herbaceous	Arboreal
44. Myrmecina americana	?	?	–	–
45. Leptothorax pergandei floridanus	x	p	x	x
46. L. texanus davisi	*	–	–	–
47. Tetramorium guineense	–	p	x	–
48. Strumigenys louisianae	–	x	–	–
49. Smithistruma bunki	–	?	–	–
50. Sm. clypeata	?	?	–	–
51. Sm. creightoni	–	?	–	–
52. Sm. dietrichi	–	x	–	–
53. Sm. ornata	–	?	–	–
54. Sm. pulchella	–	?	–	–
55. Sm. talpa	–	x	–	–
56. Trachymyrmex septentrionalis seminole	*	–	–	–
57. Dolichoderus pustulatus	–	–	x	p
58. Iridomyrmex humilis	x	–	–	–
59. I. pruinosus	p	x	–	–
60. Dorymyrmex pyramicus flavopectus	*	–	–	–
61. D. pyramicus	*	–	–	–
62. Tapinoma sessile	?	–	–	–
63. Brachymyrmex depilis	x	p	–	–
64. Camponotus castaneus	–	*	–	–
65. C. socius	*	–	–	–
66. C. nearcticus	–	x	–	p
67. C. (Colobopsis) spp.	–	–	x	p
68. C. abdominalis floridanus	x	p	x	x
69. Paratrechina longicornis	In buildings			
70. Par. arenivaga	*	–	–	–
71. Par. parvula	x	p	x	x
72. Prenolepis imparis	*	–	–	–
73. Formica archboldi	*	–	–	–
74. F. pallidefulva	*	–	–	–
75. F. schaufussi	?	–	–	–

Surface stratum.—In litter—13; in fallen log—32; in palmetto log on ground—9; in living palmetto root/trunk—16; in dead stump—22; in base of living tree—19; in base of grass clump—7.

Herbaceous stratum.—Between sawgrass blades—4; in tall grass stems—9.

Arboreal stratum.—Twig—11; small branch—14; gall—3.

Only 11 ant forms were found in over 6 of the possible 16 nesting sites. The highest number of nesting sites (14) was occupied by *Camponotus abdominalis floridanus*. Next highest was 12 nesting sites occupied by *Pheidole dentata* and *Paratrechina parvula*. It will be noted that these three ants are the same that occupy all of the stations. With the exception of *Pheidole dentata*, which occupies only 3 strata, they occupy all 4 strata also.

Leptothorax pergandei floridanus, which occupies 11 nesting sites, is the other ant found in all strata. The distribution of these ants in stations, strata, and nesting sites points to a direct correlation between the number of stations occupied and the number of strata and nesting sites occupied.

Fig. 8 shows the relation between the number of stations occupied and the number of nesting sites occupied for each ant collected more than three times. It is a scatter diagram in which the number of stations any given ant form occupies is plotted against the number of nesting sites that form occupies. An examination of this figure shows that a large number of forms are limited to from 2 to 5 stations and from 1 to 3 nesting sites. The diagram shows that the number of stations occupied by any form increases faster than the number of nesting sites occupied, indicating that the ants are more likely to be confined by nesting sites than by stations. However, the diagram goes to substantiate the premise of the preceding paragraph, in that as more stations are occupied, more nesting sites are also occupied.

ACTIVITY RELATIONSHIPS

The speed of movement of each ant form varies to some extent with changes of temperature and relative humidity. During the course of the present study, this "amount of activity" was estimated subjectively for individuals. The speed was then correlated with temperature and relative humidity readings taken at the ground surface.

The data on this subject collected during the field work proved to be complex when all of the ant forms were studied together, and in many cases when merely one form was considered. Some ants chose one extreme in physical factors in which to forage, whereas other forms chose the opposite extreme. In general, the diurnal foragers displayed a moderate amount of activity in their above-ground activities when the temperature was above 21°C. If, on the previous night, relative humidity was high and the temperature low (below 10°C), the ants were slower to resume activity the subsequent day. At the other extreme, activity has been observed from nests of *Camponotus abdominalis floridanus* at 53°C, and most of the ants have been seen foraging at temperatures above 30-35°C.

Seasonal variation in the foraging habits of several forms has also been observed. Many ant forms remain in their nests during periods of cold. On the other hand, during the winter months many forms will remain idle for a short period even though the temperature remains mild, and no frost appears at night. A notable exception is *Pheidole dentata*, which can be seen foraging even on chilly days.

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Results of a Survey of Calyptrate Flies of Medical Importance Conducted at London, Ontario During 1953[1]

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The writer (Judd, 1954) conducted a survey of mosquitoes at London, Ontario and its vicinity during 1952, and the information derived from this survey has since been used by the City of London in organizing a program of mosquito control. As a second contribution to the study of flies of medical importance in the vicinity of London it was decided to conduct a survey of calyptrate flies such as house flies, stable flies, blowflies, flesh flies, cluster flies and latrine flies during 1953. These are all flies of comparatively large size and they commonly enter houses, restaurants, public buildings, summer cottages and resort buildings. Many of them are habitually attracted to and breed in garbage, dead animal material, dung of animals and other wastes. Several of them have been known for many years to be associated with the transmission of important diseases of humans and animals such as typhoid fever, dysentery, cholera and anthrax. Invasions of the maggots of some of the species in wounds, diseased tissues and even in healthy tissues of animals and humans have frequently been observed. More recently their possible role in the dispersion and transmission of poliomyelitis virus has been investigated (Melnick, 1949; Melnick and Ward, 1945; Toomey *et al.*, 1941; Trask and Paul, 1943; Trask *et al.*, 1943). Consequently a program of control of these flies is desirable and information derived from a survey of flies occurring in a chosen locality can prove of value in establishing such a program. Surveys of flies have been made in several localities in North America, e.g. New York, N.Y. (Williams, 1954), New Haven, Conn. (Power *et al.*, 1943), Stone Mountain, Ga. (Dodge and Seago, 1954), Madison, Wisc. (Dicke and Eastwood, 1952), Rockford, Illinois (Melnick, 1949), Savannah, Ga. (Quarterman *et al.*, 1949), Charleston, W. Va. (Mail and Schoof, 1954) and, concurrently, in localities in Arizona, Kansas, Michigan, New York and West Virginia (Schoof and Savage, 1955).

Acknowledgment.—The writer wishes to express his gratitude to Mr. J. B. Hartley who aided throughout the course of the survey in collecting, identifying, sorting and counting insects and in recording data.

Methods

The flies were caught in twelve traps set out in selected localities in London

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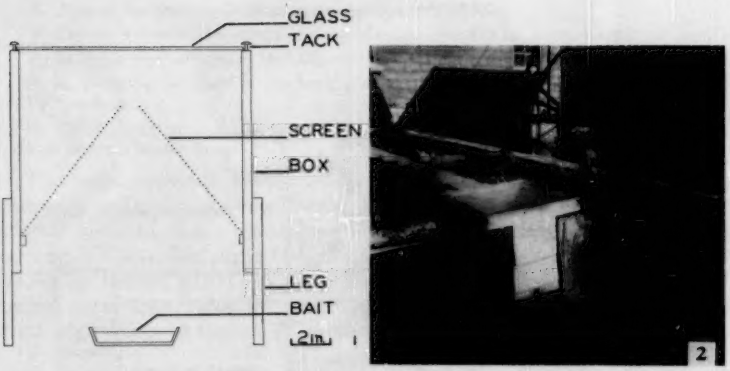


Figs. 1, 2.—1. Section of trap to show its structure; 2. Trap No. 9 in position on premises of sewage disposal plant.

and its vicinity (fig. 3). A trap (figs. 1, 2) was made from a cubical butter box of inside dimensions 12 in. x 12 in. x 12 in. The top and bottom of the box were removed and to its sides were nailed four legs which supported the box so that its lower border was four inches from the ground. A length of green plastic screening (#16 mesh) was nailed, by means of thin strips of wood, to the inside walls of the box about two inches from its lower border in such a way that the screening formed a pyramid projecting upward in the box with an opening one inch in diameter at its peak. The top of the box was covered with a glass plate so fixed in position with rows of tacks that it could be slid back to give access to the box. The trap was baited with malt extract placed in a dish four inches in diameter beneath the trap. The malt extract was "Bynin" liquid malt (Allen and Hanbury Co. Ltd., Lindsay, Ontario). Two solutions were made up: (a) a 10% aqueous solution of "Bynin" and (b) a 10% aqueous solution of ethyl alcohol. When required for use equal portions of these two solutions were mixed and the resultant mixture was used in baiting the trap. Bait was added, as required, to keep the depth of bait in the dish at about one inch.

Flies attracted to the bait would fly beneath the trap and then would travel up the lower surface of the cone of screening and through the hole in its top and so were trapped between the glass plate and the upper surface of the screen. Each cage was visited each day and the accumulated flies were removed. The glass plate was slid back about a half an inch to allow the nozzle of a "Fly-Tox" aerosol bomb to be directed into the trap and the inside of the box was sprayed lightly. When the flies in the trap had become quiescent the glass plate was removed, the trap was inverted and the flies were poured into a cyanide jar.

The twelve traps were set out at twelve places in London and its vicinity on April 13 and 14 and remained in operation until November 10. The traps were placed in the following localities (fig. 3):

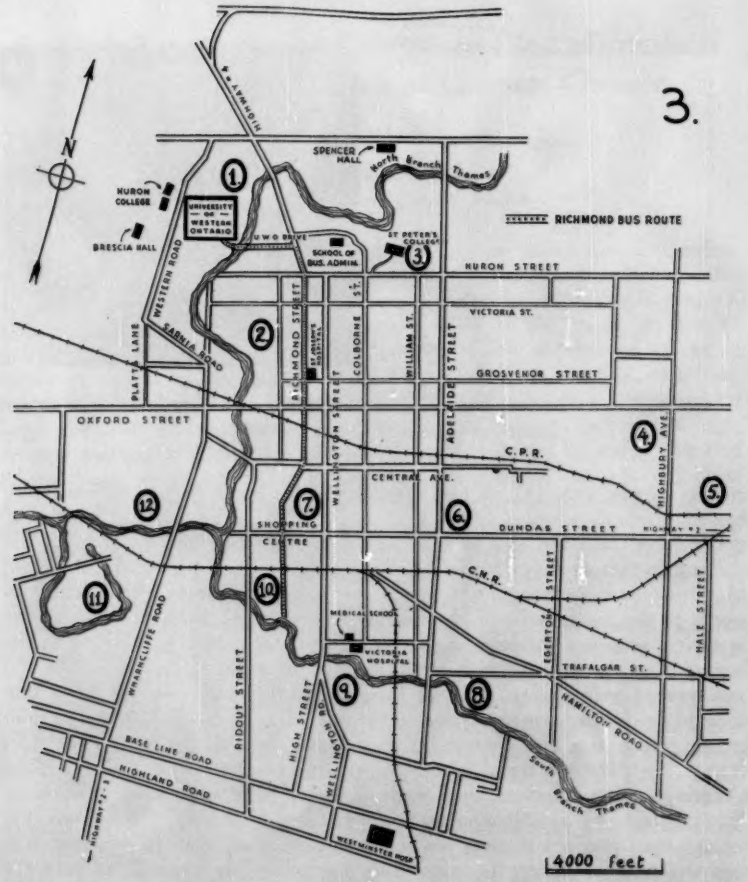


Fig. 3.—Locations of the twelve traps in London and vicinity.

1. Against the wall near service entrance of the cafeteria building, University of Western Ontario.

2. Adjacent to a stagnant backwater of the Thames River in low-lying ground next to Gibbons Park, a public park in London.

3. At the edge of a wide swamp and cat-tail marsh draining into the Thames River.

4. At the edge of a dump consisting largely of ashes and non-organic waste, surrounded by weed-grown fields and adjacent to a stable.

5. On the property of a meat-packing company adjacent to manure heaps and yards and fields harbouring cattle.

6. Among garbage cans behind a restaurant in the business district.

7. On roof (20 feet from the ground) of a building housing a hardware, restaurant and grocery in the heart of the business district.

8. Against the south wall of a large manufacturing plant.

9. On the property of a sewage-disposal plant surrounded by a city dump.

10. In stable yard of a dairy and adjacent to a meat-packing plant.

11. In a weed-grown field in low-lying ground surrounded by a stagnant backwater of the Thames River.

12. On the edge of a dump, consisting mainly of ashes and non-organic waste near the bank of the Thames River.

The traps captured a considerable assemblage of arthropods including centipedes, millipedes, sowbugs, moths, butterflies, and beetles as well as many different kinds of flies. From these were selected twenty species of flies for counting. These flies are all species included as "Diptera Calyptratae" as defined by Roback (1951) and the majority of them are known as flies of medical importance, either contaminating food, carrying pathogenic organisms or causing myiasis of tissues. The species counted were as follows:

ANTHOMYIIDAE

Muscina stabulans (Fallén)
Fannia scalaris (Fabr.)
Fannia canicularis (L.)
Pyrellia serena (Meigen)

MUSCIDAE

Musca domestica L.
Stomoxys calcitrans (L.)
Orthellia caesarion (Meigen)

CALLIPHORIDAE

Phormia regina (Meigen)
Protophormia terrae-novae (Robineau-Desvoidy)
Bufolucilia silvarum (Meigen)
Lucilia illustris (Meigen)
Phaenicia caeruleiviridis (Macquart)
Phaenicia sericata (Meigen)
Calliphora livida Hall
Calliphora terrae-novae Macquart
Calliphora vicina Robineau-Desvoidy
Calliphora vomitoria (L.)
Cynomyopsis cadaverina (Robineau-Desvoidy)
Pollenia rudis (Fabr.)

SARCOPHAGIDAE

Wohlfahrtia vigil (Walker)

In order to sort out specimens of *Wohlfahrtia vigil* it was necessary to examine all sarcophagids. A record of the number of these sarcophagids was kept. Most of them were discarded unidentified but a few were retained in spring and fall and were identified.

The twelve species of Calliphoridae were identified with keys in Hall (1947) and by comparison with a series of pinned and identified specimens received from Dr. R. J. Dicke, Department of Entomology, University of Wisconsin, who kindly contributed the specimens from his collections made during a survey of blowflies conducted at Madison, Wisconsin (Dicke and Eastwood, 1952). The two species of *Fannia* were identified with keys in Malloch (1924, 1924a). Mr. G. E. Shewell, Systematic Entomology, Department of Agriculture, Ottawa, kindly identified representative specimens of *Wohlfahrtia vigil, Orthellia caesarion* and *Pyrellia serena*. The other Sarcophagidae were identified by Dr. H. R. Dodge, Communicable Disease Centre, U.S. Public Health Service, Savannah, Georgia. *Muscina stabulans, Musca domestica* and *Stomoxys calcitrans* were identified with keys in textbooks on Medical Entomology, e.g. Matheson (1950).

The total count of flies of each species collected from each trap is presented in table 1.

TABLE 1.—Numbers of flies collected in traps during 1953

	Trap numbers						
	1	2	3	4	5	6	7
Muscina stabulans	125	8	169	377	1,131	490	387
Fannia scalaris	19	1	11	36	128	5	12
F. canicularis	6	7	100	287	207	34	53
Pyrellia serena	3	257	646	142	44	17	22
Musca domestica	552	4	142	40	3,389	336	230
Stomoxys calcitrans	1	0	0	5	16	5	0
Orthellia caesarion	0	0	4	1	1	0	0
Phormia regina	25	161	318	1,374	1,344	222	331
Protophormia terrae-novae	0	1	1	24	63	10	9
Bufolucilia silvarum	0	99	209	77	55	7	7
Lucilia illustris	123	366	2,757	1,581	997	831	145
Phaenicia caeruleiviridis	1	20	36	9	8	2	4
P. sericata	547	214	531	705	2,053	34,547	3,412
Calliphora livida	1	373	167	300	146	22	33
C. terrae-novae	1	15	35	36	25	10	5
C. vicina	28	25	80	635	225	225	162
C. vomitoria	0	2	36	11	13	1	6
Cynomyopsis cadaverina	75	925	837	1,096	857	216	549
Pollenia rudis	698	366	692	2,016	2,270	302	1,162
Wohlfahrtia vigil	0	0	0	2	0	0	0
TOTAL	2,205	2,844	6,771	8,754	12,972	37,282	6,529

	Trap numbers						
	8	9	10	11	12	Total males	Total flies
Muscina stabulans	63	645	284	128	55	1,675	3,862
Fannia scalaris	2	15	1	13	6	127	249
F. canicularis	22	100	32	146	49	531	1,043
Pyrellia serena	0	38	0	87	214	694	1,470
Musca domestica	24	76	820	255	30	2,642	5,898
Stomoxys calcitrans	0	8	3	193	1	110	232
Orthellia caesarion	0	0	0	109	23	57	138
Phormia regina	9	376	63	719	368	2,113	5,310
Protophormia terrae-novae	0	15	4	4	0	50	131
Bufolucilia silvarum	3	24	1	31	26	407	539
Lucilia illustris	73	1,270	302	2,740	342	3,764	11,527
Phaenicia caeruleiviridis	7	27	5	6	5	54	130
P. sericata	783	3,398	21,325	5,631	244	29,972	73,390
Calliphora livida	4	224	4	46	44	689	1,364
C. terrae-novae	1	19	2	20	25	46	194
C. vicina	57	92	105	104	24	920	1,762
C. vomitoria	1	3	0	9	12	10	94
Cynomyopsis cadaverina	129	131	1,259	684	798	3,238	7,556
Pollenia rudis	85	788	365	2,866	786	5,854	12,396
Wohlfahrtia vigil	0	0	0	0	0	2	2
TOTAL	1,263	7,249	24,575	13,791	3,052		127,287
Other Sarcophagidae							15,688
TOTAL							142,975

ACCOUNT OF TOTAL CATCH

During the period April 13 to November 10, 142,975 flies were caught in the traps. The twenty species of flies selected for counting accounted for 127,287 of this total and the remainder, 15,688, was comprised of other sarcophagids (table 1). During April, May and June the catch of flies was relatively light (fig. 4). The peak of abundance occurred toward the end of July with the maximum daily catch, 4,666 flies, occurring on July 24. Further peaks of abundance occurred in August and September. The population fell off in October and November but with sporadic upsurges coinciding with warm days in those months. The catch of flies varied very considerably from one trap to another.

Trap 6 (37,282 flies).—This trap yielded more than one-quarter of the total number of flies and of these the great majority were *Phaenicia sericata*. The trap was placed among several battered garbage cans, often lidless at times through the summer, together with miscellaneous boxes and tins of garbage added from time to time. It has been demonstrated by several workers (Anon., 1953; Williams, 1954) that in cities garbage in containers is a major breeding site for domestic flies. Quarterman *et al.* (1949) found in the survey conducted at Savannah, Ga., that garbage cans were the second most important source of flies and that 60% of all garbage containers actively produced flies in the accumulation of sludge in the cans.

Trap 10 (24,575 flies).—This trap, in the stable-yard of a dairy and near a packing plant, yielded the second greatest number of flies. It was adjacent to a barn containing manure and straw. The great majority of the flies were *Phaenicia sericata* but included considerable numbers of *Musca domestica*.

Trap 11 (13,791 flies). At this trap, in a weed-grown field surrounded by a sluggish body of water, the greatest concentration of flies occurred in

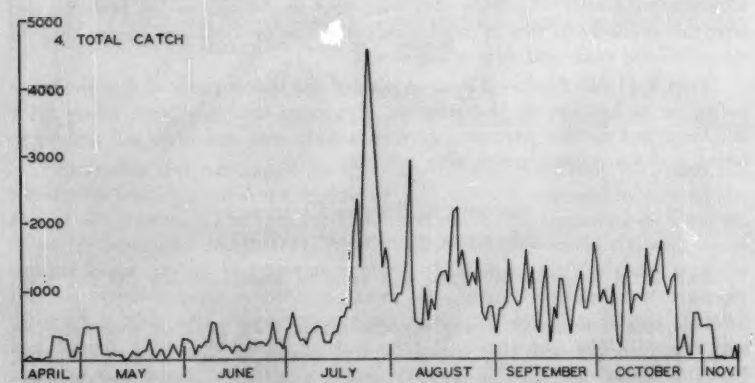


Fig. 4.—Number of all Anthomyiidae, Muscidae, Calliphoridae and Sarcophagidae trapped daily during 1953.

the fall, with the largest weekly catch, 3,565 flies, in the week of October 13 to 19. *Phaenicia sericata* predominated in this trap and *Pollenia rudis* and *Lucilia illustris* were present in large numbers.

Trap 5 (12,972 flies).—In this trap, in the premises of a meat-packing plant including a large manure heap and yards for keeping cattle, the house fly, *Musca domestica*, predominated. This fly no doubt bred in the manure. Three other common species were *Pollenia rudis*, *Phormia regina* and *Muscina stabulans*.

Trap 4 (8,754 flies).—In this trap, set in a dump surrounded by wet meadows and fields, the predominant species was *Pollenia rudis*.

Trap 9 (7,249 flies).—The predominant flies in this trap, in the vicinity of a city dump, were *Phaenicia sericata* and *Lucilia illustris*.

Trap 3 (6,771 flies).—In this trap, set on the edge of a marsh, the predominant fly was *Lucilia illustris* and the blowfly *Bufolucilia silvarum* occurred here in its greatest numbers.

Trap 7 (6,529 flies).—*Phaenicia sericata* predominated in this trap set on a roof above stores and restaurants in the business district. Conditions here were comparable to those at Trap 6 except that the garbage cans were kept in more sanitary condition and the trap was set farther from them.

Trap 12 (3,052 flies).—In this trap, on a dump surrounded by damp fields, about half the catch was made up of *Pollenia rudis* and *Cynomyopsis cadaverina*. The greatest number of flies were trapped in the fall with the largest weekly catch in the week of October 20 to 26. During the summer the trap was densely overshadowed by the leafage of small trees and few flies were trapped, but with the dropping of the leaves the catch increased.

Trap 2 (2,844 flies).—The predominant flies in this trap, set on the border of a pond in a park, were the bluebottles *Cynomyopsis cadaverina* and *Calliphora livida*.

Trap 1 (2,205 flies).—This trap was set near the service entrance to the University cafeteria. Garbage cans were kept in the rear of the building and were not available to flies in large numbers. The predominant species trapped were *Pollenia rudis* and *Musca domestica*.

Trap 8 (1,263 flies).—This trap yielded the lowest catch of flies doubtless owing to its location on the premises of a large steelware plant where brick buildings and cement pavement covered a wide area and little soil and vegetation and no organic waste were present.

Account of Species Collected

MUSCINA STABULANS (Fallén)

April 22 to November 10: 3,862 flies (peak of abundance—July 26: 119 flies) (fig 5).

This species occurred throughout the season. Its peak of abundance, in mid-July, coincides with that found for this species in New York (Williams, 1954). Schoof and Savage (1955) found that it accounted for no more than 5.1% of the flies trapped in five cities and Dodge and Seago (1954) found it scarce on mountain tops in Georgia. In London it occurred in

greatest numbers on the premises of the packing company (trap 5) where it doubtless bred in the manure.

FANNIA SCALARIS (Fabr.)

May 1 to November 3: 249 flies (females not counted between June 1 and July 12) (peak of abundance—July 29: 7 flies) (fig. 6).

This species was found in all traps, with more than half the number occurring in Trap 5. This concentration in Trap 5 was probably due to the presence of manure heaps for it is in this material that the larvae of *F. scalaris* are commonly found. The peak of abundance occurred at the end of July and the population remained high into the fall.

FANNIA CANICULARIS (L.)

April 28 to November 10: 1,043 flies (females not counted between June 1 and July 12) (peaks of abundance—May 30: 26 flies; September 19: 35 flies) (fig. 7).

This fly was collected in all traps and predominated in Traps 4 and 5, doubtless owing to the presence of manure heaps in the vicinity. It was present throughout the season, occurring in greatest abundance in spring and fall. Williams (1954) found it scarce in New York. Dodge and Seago (1954) captured it on mountains in Georgia.

PYRELLIA SERENA (Meigen)

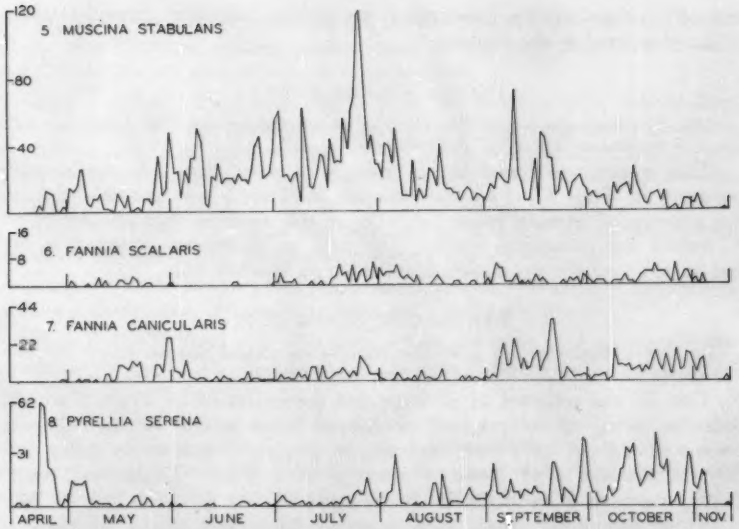
April 15 to November 10: 1,470 flies (peaks of abundance—April 22: 62 flies; October 20: 44 flies) (fig. 8).

This species occurred throughout the season and was most abundant in April and October at Traps 2 and 3. It is a species that passes the winter in hibernation as an adult (Holmquist, 1928), a circumstance which accounts for its abundance in spring and fall. Holmquist (1928) found it in hibernation in logs and stumps in a floodplain. At London it was found in just such a situation, for the vicinity of Trap 2 was flooded in the spring and the vicinity of Trap 3 was also flooded in the spring and remained swampy throughout the year. Dodge and Seago (1954) found that it was one of the commoner anthomyiid flies on mountain tops in Georgia.

MUSCA DOMESTICA (L.)

May 16 to November 4: 5,898 flies (peak of abundance—October 23: 329 flies) (fig. 9).

House flies did not appear in the traps till the middle of May and the population was light until the middle of July when it rose rapidly toward the end of the month. The greatest concentration of flies occurred in October. Most of them were caught in Traps 5 and 10 which were in the vicinity of manure heaps, stables and animal remains. Matheson (1950) states that the favorite breeding place is horse manure. Maximum densities of this species occurred in July and August in surveys conducted in West Virginia (Mail and Schoof, 1954), in New Haven, Conn. (Power *et al.*, 1943) and at four localities in Kansas, W. Virginia, New York and Michigan (Schoof and Savage, 1955). None of these surveys indicated that it is regularly predominant in the population.



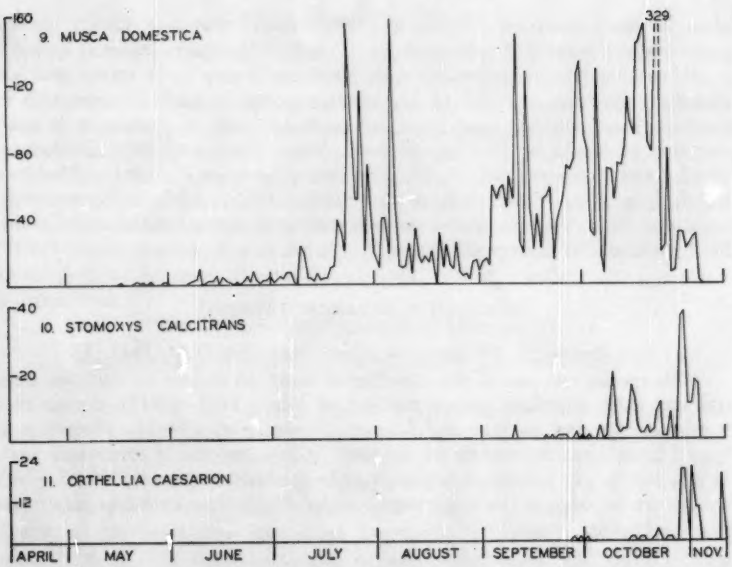
Figs. 5-8.—Number of flies trapped daily during 1953. 5. *Muscina stabulans;* 6. *Fannia scalaris;* 7. *Fannia canicularis;* 8. *Pyrellia serena.*

The appearance of *Musca domestica* in large numbers in July and August, as reported in other surveys (Mail and Schoof, 1954; Power *et al.*, 1943; Schoof and Savage, 1955), was also noticeable at London. The greatest numbers of house flies occurred at London, however, in October. The likelihood is that in the vicinity of Traps 5 and 10, where the flies were present in greatest numbers, conditions were such that the flies could assemble there and even breed during fall and winter, for dairy barns, stables and sheds were present there. Matthysse (1945) reported breeding of *M. domestica* in dairy barns and heated barns in northern New York and considered indoor propagation of this species as its most important method of overwintering. The concentration of flies in restaurants, stables and warm buildings was stressed by Hewitt (1915).

STOMOXYS CALCITRANS (L.)

September 10 to November 3: 232 flies (peak of abundance—October 30: 38 flies) (fig. 10).

The biting stable fly was trapped only in the fall. Most of the flies were caught in Trap 11. Matheson (1950) points out that this fly frequents human habitations, particularly in the late summer and autumn and that it is a "lover of the open" which would probably account for its predominance in Trap 11 set on a dump bordering flats and fields along the Thames River. This species was found to be relatively scarce in New York (Williams, 1954) and on mountains in Georgia (Dodge and Seago, 1954).



Figs. 9-11.—Number of flies trapped daily during 1953. 9. *Musca domestica;* 10. *Stomoxys calcitrans;* 11. *Orthellia caesarion.*

ORTHELLIA CAESARION (Meigen)

September 27 to November 10: 138 flies (peak of abundance—November 1: 22 flies) (fig. 11).

This fly was trapped only in the fall and the great majority of the specimens were caught in Trap 11.

PROTOPHORMIA TERRAE-NOVAE (Robineau-Desvoidy)

April 16 to October 18: 131 flies (peak of abundance—July 24: 21 flies) (fig. 12).

This fly was comparatively scarce in the collections and reached its peak of abundance toward the end of July and was trapped in greatest numbers in Trap 5. Hall (1947) reports that it is an early spring species in the United States, although occasional specimens are collected in summer. It was, however, collected in greatest numbers in July at Madison (Dicke and Eastwood, 1952) and in June and July at New Haven (Power *et al.*, 1943).

PHORMIA REGINA (Meigen)

April 15 to November 10: 5,310 flies (peak of abundance—July 25: 251 flies) (fig. 13).

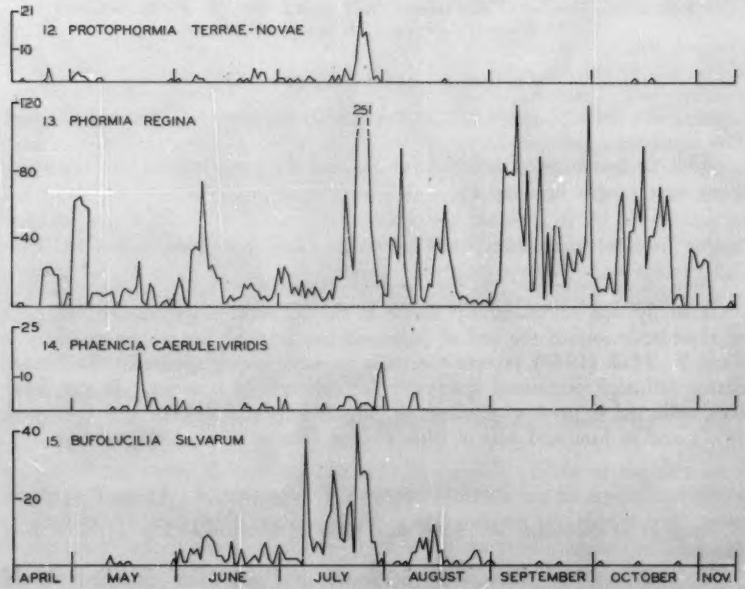
This fly occurred throughout the season and was most abundant toward the end of July. It was present in greatest numbers in Traps 4 and 5. Hall (1947) records that when fresh blood is present in abbatoirs this species

often becomes abundant. Melnick (1949) found that this species yielded positive tests for virus of poliomyelitis. Hall (1947) reports that it is typically a cold-weather blowfly, becoming most abundant during early spring and less abundant with the approach of hot weather except at high altitudes and in northern areas. It has been found to reach its peak of abundance in mid-summer, as it did at London, in New York (Williams, 1954), Madison (Dicke and Eastwood, 1952), New Haven (Power *et al.*, 1943), Michigan and Cohoes, New York (Schoof and Savage, 1955), while in Kansas, Arizona and West Virginia it was most prevalent in spring (Mail and Schoof, 1954; Schoof and Savage, 1955).

BUFOLUCILIA SILVARUM (Meigen)

May 11 to October 25: 539 flies (peak of abundance—July 23: 42 flies) (fig. 15).

This species was one of the blowflies of lesser occurrence in the collections and was most abundant toward the end of July. Hall (1947) reports that it is most abundant in June and July and Power *et al.* (1943) collected it at New Haven after the middle of August. It is a parasite of frogs and toads (Hall, 1947). In London it was trapped in greatest numbers in Trap 3 which was set on the edge of the large swamp where *B. silvarum* probably parasitized frogs and toads.



Figs. 12-15.—Number of flies trapped daily during 1953. 12. *Protophormia terrae-novae;* 13. *Phormia regina;* 14. *Phaenicia caeruleiviridis;* 15. *Bufolucilia silvarum.*

LUCILIA ILLUSTRIS (Meigen)

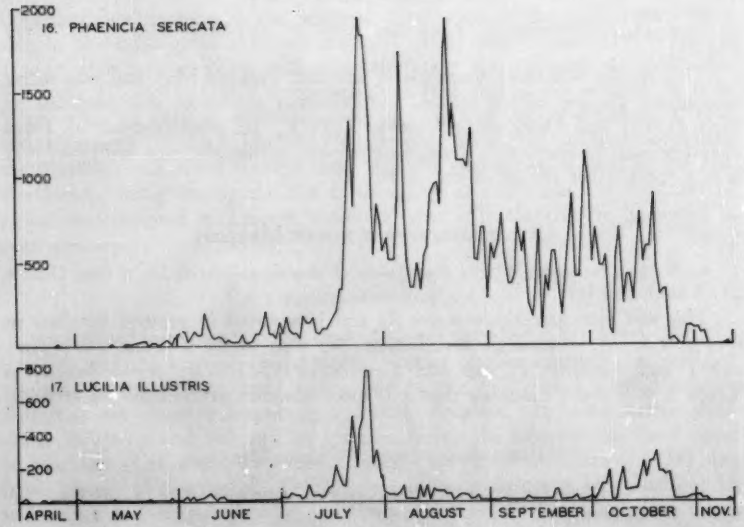
April 14 to November 10: 11,527 flies (peak of abundance—July 25: 779 flies) (fig. 17).

These blowflies were well distributed among all the traps and predominated in Traps 3 and 11. These two traps were on the outskirts of London in areas occupied by swamp, woods and fields and the presence of *L. illustris* in these areas is in accord with Hall's estimate (1947) that it is an "open woodland and meadow species." Its peak of abundance was at the end of July, with considerable numbers occurring in October. Dicke and Eastwood (1952) found its peak of abundance in July at Madison and Williams (1954) recorded it as between the middle of June and the middle of September in New York.

PHAENICIA CAERULEIVIRIDIS (Macquart)

May 12 to October 2: 130 flies (peaks of abundance—May 20: 17 flies; July 30: 14 flies) (fig. 14).

This species was one of the scarcer blowflies in the collections and was caught in all traps, predominantly in Trap 3. Its relative abundance in May is in accord wtih the findings of Mail and Schoof (1954). Schoof and Savage (1955) found that it was the least abundant of the species of *Phaenicia* in the centres investigated by them but Dodge and Seago (1954) found it one of the commoner species on mountains in Georgia. Hall (1947) records that it is a common species in woods and fields but not abundant about houses. At London, its predominance in Trap 3 bears out Hall's conclusions.



Figs. 16, 17.—Number of flies trapped daily during 1953. 16. *Phaenicia sericata;* 17. *Lucilia illustris.*

PHAENICIA SERICATA (Meigen)

April 25 to November 10: 73,390 flies (peak of abundance—July 24: 1,956 flies) (fig. 16).

This was the fly of greatest abundance in the collections, accounting for more than half the total catch of the twenty species counted. Hall (1947) records that it is the most abundant species of *Phaenicia* in North America, occurring most frequently in collections in the northern United States and southern Canada. Its peak of abundance was in the latter part of July and the population remained high during the rest of the season. This seasonal distribution is the same as that found in Madison (Dicke and Eastwood, 1952) and in the centres investigated by Schoof and Savage (1955). Dicke and Eastwood (1952), Schoof and Savage (1955), Williams (1954) and Power *et al.* (1943) found it among the most abundant of flies collected, particularly around cities, but Dodge and Seago (1954) found it relatively scarce on mountains in Georgia. It was one of the flies found positive for virus of poliomyelitis by Melnick (1949).

P. sericata was caught in all traps at London, almost half the flies being in Trap 6. This trap was placed among uncovered cans and boxes of garbage which attracted great numbers of *P. sericata* and the presence of this fly there is in accord with Hall's conclusion (1947) that "adults may be collected in abundance on almost any kind of garbage, particularly when it is mixed with meats of various sorts and with damaged fruits."

CALLIPHORA LIVIDA Hall

April 14 to November 2: 1,364 flies (peak of abundance—May 4: 117 flies) (fig. 20).

This species was most abundant in the first week of May and was scarce throughout the rest of the season, a distribution similar to that recorded by Hall (1947) and Dicke and Eastwood (1952). Its predominance in Traps 2 and 4 and its scarcity in traps located well within the city indicated that it is a species that frequents the open.

CALLIPHORA TERRAE-NOVAE Macquart

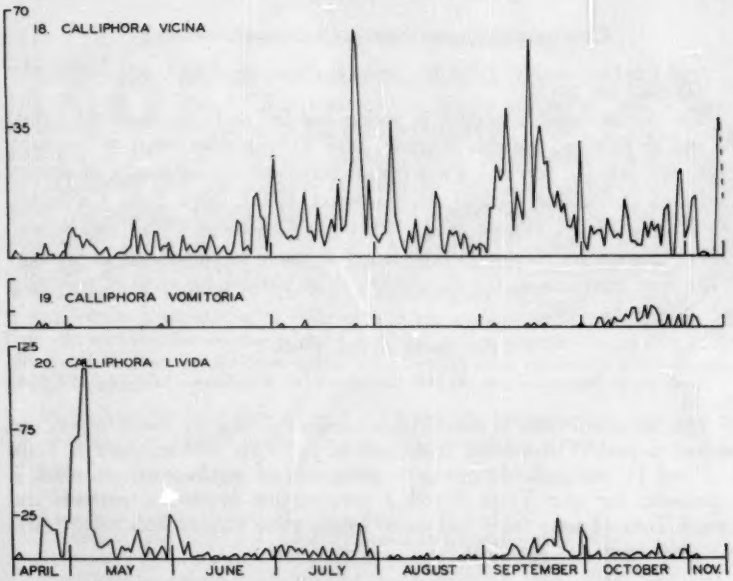
April 22 to November 3: 194 flies (peaks of abundance—April 23: 6 flies; October 21: 8 flies) (fig. 21).

This was a comparatively scarce fly and it occurred in greatest numbers in spring and fall, a seasonal distribution like that in New York (Williams, 1954) and Madison (Dicke and Eastwood, 1952). Its predominance in Traps 3, 4, 5 and 12 indicate that it is most common in the open countryside.

CALLIPHORA VICINA Robineau-Desvoidy

April 15 to November 10: 1,762 flies (peaks of abundance—July 25: 64 flies; September 15: 61 flies) (fig. 18).

This species occurred in collections throughout the season, showing two peaks of abundance and maintaining a high population well into November.



Figs. 18-20.—Number of flies trapped daily during 1953. 18. *Calliphora vicina;* 19. *Calliphora vomitoria;* 20. *Calliphora livida.*

Considerable differences in the seasonal distribution of the species are noticeable in the findings of different authors. Mail and Schoof (1954) found it most abundant in May, with scarcity during the summer, at Charleston. Williams (1954) found it comparatively scarce during the summer in New York, while its peak of abundance was in June and July at Madison (Dicke and Eastwood, 1952). Hall (1947) records that it is uncommon during the summer. All these authors show that the population is high in the fall, this blowfly being among the last to disappear at that time. In London, *C. vicina* predominated in Trap 4, indicating that it is a species to be found in open country.

CALLIPHORA VOMITORIA (L.)

April 22 to November 3: 94 flies (peak of abundance—October 21: 7 flies) (fig. 19).

This was the scarcest of the twenty species of flies counted. It was particularly in evidence in early spring and in the fall. Hall (1947) records that it is not common anywhere in North America. Its comparative abundance in spring and fall and its scarcity during the summer has been noted at Madison (Dicke and Eastwood, 1952), New York (Williams, 1954) and New Haven (Power *et al.*, 1943). It was quite abundant in collections on mountains in Georgia (Dodge and Seago, 1954). In London it was found in greatest numbers in traps on the outskirts of the city (Traps 3, 4, 5, 12) and was scarce or not present at all in traps within the city.

CYNOMYOPSIS CADAVERINA (Robineau-Desvoidy)

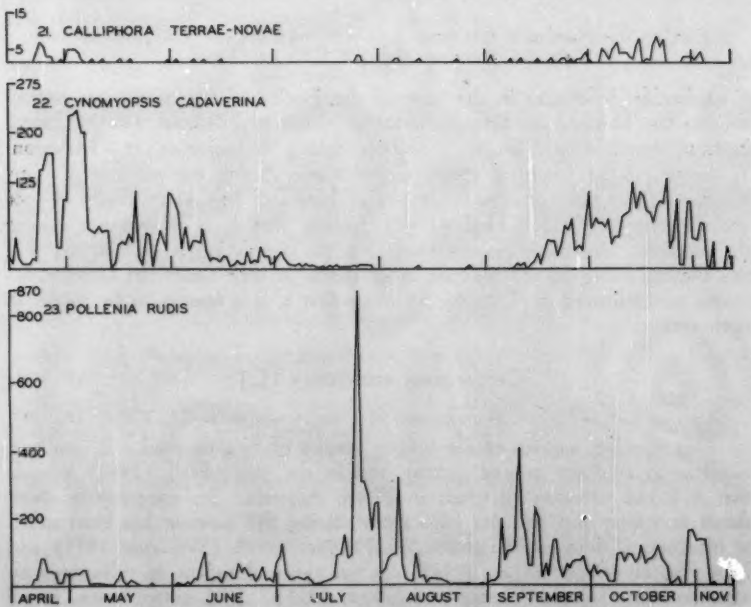
April 3 to November 10: 7,556 flies (peaks of abundance—May 3: 245 flies; October 23: 133 flies) (fig. 22).

This fly was most abundant in spring and fall and became scarce during the end of July and through August. Hall (1947) describes it as "an early spring and late fall species," a description borne out by the results of surveys conducted at Madison (Dicke and Eastwood, 1952), New York (Williams, 1954), New Haven (Power *et al.*, 1943) and Charleston (Mail and Schoof, 1954). Dodge and Seago (1954) found it scarce on mountains in Georgia. It has been found, in its fall population, to be positive for virus of poliomyelitis (Melnick, 1949).

POLLENIA RUDIS (Fabr.)

April 20 to November 10: 12,396 flies (peak of abundance—July 24: 869 flies) (fig. 23).

This fly was present in considerable numbers during the whole season and reached its peak of abundance at the end of July. Its predominance in Traps 4, 5 and 11 was probably owing to prevalence of earthworms, on which it is parasitic, for near Traps 4 and 5 were manure heaps and pastures and around Trap 11 were fields and damp banks, these various sites being places in which worms are prevalent.



Figs. 21-23.—Number of flies trapped daily during 1953. 21. *Calliphora terrae-novae;* 22. *Cynomyopsis cadaverina;* 23. *Pollenia rudis.*

WOHLFAHRTIA VIGIL (Walker)

Only two of these flies were caught, one male on July 12 and one male on July 14, both in Trap 4. The habit of this species causing myiasis of tissues of human infants and animals has been investigated by Ford (1936), Kingscote (1932, 1935) and Walker (1931, 1937). Ford (1936) and Walker (1931) record that the adult is attracted to milk, sugar, flowers and other sweet substances. One of the two flies trapped at London was carrying pollinia of milkweed (Judd, 1955). Ford (1936) found that the adult flies were particularly to be found along railway tracks and offered the explanation that the warmth of the tracks attracted the flies. At London, Trap 4 was within a quarter of a mile of a main railway track leading into the city. It was also set on the edge of a dump of non-organic material in which ashes and clinkers predominated and which could thus provide a warm surface in hot weather.

In addition to *Wohlfahrtia vigil* the following sarcophagids, identified by Dr. Dodge, were caught in the traps during the periods shown.

Bellieria melanura (Mg.)—14 ♂ ♂, 6 ♀ ♀: June 1 to September 23.
Blaesoxiphotheca sp.—2 ♀ ♀: September 17, 19.
Boettcheria bisetosa Parker—1 ♀: June 7.
B. cimbicis (Tns.)—72 ♂ ♂, 33 ♀ ♀: June 1 to September 29.
B. latisterna Parker—4 ♂ ♂, 5 ♀ ♀: June 1 to September 23.
Brachicoma sarcophagina (Tns.)—1 ♂: June 4.
Chaetoravinia latisetosa (Parker)—2 ♂ ♂, 5 ♀ ♀: June 1 to September 14.
Metoposarcophaga importuna Wlk.—3 ♂ ♂, 6 ♀ ♀: June 1 to September 14.
Oxysarcodexia cingarus (Ald.)—4 ♂ ♂, 1 ♀: June 4 to September 15.
O. ventricosa (Wulp)—4 ♂ ♂, 12 ♀ ♀: June 6 to September 29.
Ravinia pusiola (Wulp)—11 ♂ ♂, 9 ♀ ♀: June 2 to September 29.
R. querula (Wlk.)—28 ♂ ♂, 33 ♀ ♀: June 2 to October 1.
Sarcophaga aldrichi Parker—1 ♀: June 3.
S. argyrostoma (R-D.)—2 ♂ ♂, 2 ♀ ♀: June 1 to September 20.
S. bullata Parker—32 ♂ ♂, 26 ♀ ♀: June 1 to September 23.
S. crassipalpis (Mcq.)—2 ♂ ♂: June 4, September 16.
S. haemorrhoidalis (Fall.)—13 ♂ ♂, 9 ♀ ♀: June 1 to September 29.
S. hesterna Reinhard—1 ♂, 1 ♀: June 2, 7.
S. l'herminieri (R-D.)—13 ♂ ♂, 31 ♀ ♀: June 1 to September 29.
S. nearctica Parker—10 ♂ ♂, 13 ♀ ♀: June 1 to September 26.
S. sarracenioides Aldr.—1 ♀: September 17.
Sarcotachinella sinuata (Mg.)—4 ♂ ♂, 2 ♀ ♀: June 1 to September 29.

SUMMARY

During the period April 13 to November 10, 1953 142,975 flies were trapped in twelve traps baited with malt extract and set out in twelve localities in London, Ontario and its vicinity. The flies were removed from the traps each day and sorted and counted according to species and sex. Twenty species in the families Anthomyiidae, Muscidae, Calliphoridae and Sarcophagidae were counted and their times of occurrence throughout the season and the times of their greatest abundance were recorded. The species counted were *Muscina stabulans, Fannia scalaris, F. canicularis, Pyrellia serena, Musca domestica, Stomoxys calcitrans, Orthellia caesarion, Phormia regina, Protophormia terrae-novae, Bufolucilia silvarum, Lucilia illustris, Phaenicia caeruleiviridis,*

P. sericata, Calliphora livida, C. terrae-novae, C. vicina, C. vomitoria, Cynomyopsis cadaverina, Pollenia rudis, and *Wohlfahrtia vigil.* The greatest abundance of flies occurred toward the end of July. Most of the flies were taken in traps set in the vicinity of garbage cans and in the premises of packing plants and dairies which harbored animals.

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The Genus Procambarus in Louisiana (Decapoda, Astacidae)

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This is the third of a series of four papers on the crawfishes of Louisiana. The first two, on the genera *Cambarellus* and *Orconectes* respectively (Penn, 1950, 1952), should be referred to for the introductory remarks and a key to the abbreviations denoting disposition of the specimens. To the latter add: CM=Carnegie Museum, Pittsburgh, Pa., and ASMNH=Alabama State Museum of Natural History, Tuscaloosa, Ala.; and delete UMMZ (University of Michigan, Museum of Zoology) of which the entire crustacean collections have been transferred to the USNM.

A number of habitat factors (e.g., depth of water, flow, shaded vs. exposed, etc.) are routinely recorded by the writer for each collection made. However, other collectors who have given crawfish to the Tulane collection have not always recorded data on the same factors. Hence, in summarizing habitat data for each species the number of lots (=collections) analyzed is in each case represented by somewhat less than complete data.

Procambarus Ortmann, 1905

Diagnosis.—First pleopod of form I male terminating in from two to five distinct parts which may be truncate, platelike or spiniform; shoulder present or absent on cephalic surface of distal third; if the pleopod terminates in only two parts this shoulder is always present. In the male, hooks are present on the ischiopodites of the third or of the third and fourth pereiopods.

The genus is divided into a number of "sections," of which three are represented in Louisiana: *Blandingii, Hinei* and *Barbatus.*

Blandingii Section

Diagnosis.—Cephalodistal margin of first pleopod of male never with a ridge or knob-like prominence unless it is a part of one of the terminal processes; distad the appendage may be directed straight or caudad; mesial process generally bent (either caudodistad or caudolaterad); a crescentic terminal protuberance never present; cephalic process when present arises from cephalic or cephalolateral margin in all species except those of the *planirostris* subgroup in which it arises from the mesial side of the central projection; hooks present on ischiopodites of third and fourth pereipods [after Hobbs (1942) as amended by Penn (1953c)].

The *Blandingii* section is divided into a number of "groups", of which the *blandingii* and *spiculifer* groups are represented in the state.

BLANDINGII GROUP

Diagnosis.—Areola long, relatively narrow or obliterated; rostrum may or may not bear lateral spines (if lateral spines are absent, then the margins are always interrupted).

Four species of this group are known to occur in Louisiana.

PROCAMBARUS BLANDINGII ACUTUS (Girard)

Cambarus acutus Girard, 1852, Proc. Acad. Nat. Sci. Phila. 6:91; *Cambarus stygius* Bundy, 1876, Bull. Ill. Mus. Nat. Hist. 1:3; *Cambarus blandingii* var *acuta* Girard, Faxon, 1884, Proc. Amer. Acad. Arts & Sci. 20:136; *Cambarus blandingii acutus* Girard, Faxon, 1890, Proc. U. S. Nat. Mus. 12:619; *Procambarus blandingii acutus* (Girard) Hobbs, 1942, Amer. Midl. Nat. 28:342.

Diagnosis.—Rostrum with very small lateral teeth present near tip (absent in some specimens); areola narrow, but definitely open; chela long and slender; one lateral spine on each side of cephalothorax. First pleopod of form I male reaching to coxopodite of third pereiopod and ending in four distinct parts: mesial process long and spiniform and directed laterodistad; cephalic process blade-like, corneous, compressed, and directed caudodistad; caudal element and central projection acute, bladelike, corneous, compressed, and directed caudodistad.

Type locality.—"Affluent of Mobile River, Kemper County, Miss."; types probably destroyed in the Chicago fire of 1871, questionable paratypes are in the ANS according to Faxon (1914).

Specimens examined.—In Louisiana this is an exceedingly common form; I have examined several thousand specimens from localities in 52 of the 64 parishes as follows: Acadia, Ascension, Avoyelles, Beauregard, Bienville, Bossier, Calcasieu, Caldwell, Cameron, Catahoula, Claiborne, Concordia (USNM), DeSoto (USNM, TU), East Baton Rouge (HHH, TU), East Feliciana, Evangeline, Franklin, Grant (USNM, HHH, TU), Iberia, Iberville (MCZ, TU), Jackson, Jefferson (USNM, TU), Lafayette, Lafourche (USNM), Lincoln, Livingston, Morehouse, Natchitoches (USNM, TU), Orleans (USNM, MCZ, TU), Ouachita, Pointe Coupee, Rapides (HHH, TU), Richland, Sabine (USNM, TU), St. Bernard (USNM), St. Charles, St. Helena, St. James, St. Landry, St. Mary, St. Tammany (USNM, HHH, TU), Tangipahoa (USNM, HHH, TU), Tensas, Terrebonne (USNM, MCZ), Union, Vermilion, Vernon (USNM, TU), Washington, Webster, West Baton Rouge (HHH, TU), West Feliciana and Winn (USNM, TU).

Previously it had been recorded from only seven parishes: Cameron (Penn, 1953a), DeSoto (Ellis, 1919), East Carroll (Hagen, 1870), Grant (Penn, 1946), Orleans (Hagen, 1870; Faxon, 1885), St. Tammany (Smith, 1953; Bick et al, 1953), and Tangipahoa (Faxon, 1885).

Life history.—The seasonal cycle of this common crawfish has not been studied anywhere in its wide geographic range. An analysis of the seasonal distribution of size groups of 982 Louisiana specimens preserved in the Tulane collection makes possible a few statements on its life cycle.

Form II males begin increasing in number in January, reach a peak of abundance about the end of March, and then decrease through July. Few are collected during the remainder of the year. Presumably the decrease in number of form II males is caused by the molting of most of them to form I as warm

weather approaches. Form I males and mature females increase in number from December through July when a peak is reached, and then they also are rarely found in the water collections. Judging from the number of females with sperm plugs in their annuli, copulation may take place early during this same six month span, but as the number of mature males and females increase the tempo of mating rises also and reaches a peak in June and July. Growth of oocytes proceeds at a uniform rate from February (range: 0.2 to 0.4 mm diameter) through July (range: 0.4 to 0.6 mm diameter). In August the growth rate is much more rapid (range: 0.7 to 1.5 mm diameter) indicating a late summer and early fall spawning period. Ovigerous females have not been collected, but females carrying young were found in October and January (one specimen each) in shallow burrows under logs in damp places. Since mature females are rarely collected from September through December, egg laying must be accomplished in burrows, perhaps at the edges of drying ponds and streams. Small juveniles (less than 15 mm cephalothorax length) appear most abundantly in the water collections from December through February.

That this does not represent the annual cycle for *P. b. acutus* in all parts of its range is apparent from the records of ovigerous females given by Turner (1926), who found females carrying eggs or young in March, July and September in Ohio and Indiana. He concluded that there is no definite season when reproduction occurs in this species and this may well prove to be true in the northern part of its range. No other records of ovigerous females are known to the writer.

Ecological observations.—An analysis of the data on 160 lots of this crawfish from Louisiana is summarized briefly in the table below.

Habitat		Percent of Total Collections
Temporary situations:		39.9
Ditches (mostly roadside)	26.2	
Pineland sloughs	9.4	
Burrows	3.7	
On land (migrating?)	0.6	
Permanent situations:		60.1
Creeks and rivers	25.0	
Ponds and borrow pits	26.3	
Swamps and swamp pools	8.8	

The various physical and biological factors in all habitats combined may be summarized in the statement that *P. b. acutus* occurs most frequently in shallow water, i.e., less than 15 inches deep (74%), which is turbid (53%), permanent (60%), static (72%), and exposed to full sunlight (60%). Most of the collections were from habitats with mud bottoms (71%), and with aquatic vegetation present (72%). The aquatic plants most commonly found in these places, in order of frequency of occurrence, were *Polygonum* spp., *Jussiaea* spp., *Myriophyllum* sp., *Juncus* spp., *Achyranthes philoxeroides*, *Eleocharis* spp., *Tradescantia* sp., *Pontederia* sp., *Sagittaria* spp., *Utricularia* spp., *Saururus* sp. and *Iris* spp.

PROCAMBARUS BIVITTATUS Hobbs

Procambarus bivittatus Hobbs, 1952, Univ. Fla. Publ., Biol. Sci. Ser. 3(2):96.

Diagnosis.—Rostrum long, with lateral spines; areola open but very narrow; a single, large lateral spine on each side of cephalothorax. First pleopod of form I male reaching coxopodite of third pereiopod and terminating in four distinct parts: mesial process blade-like with an acute tip and directed caudodistad; cephalic process lamelliform, compressed, caudodistal tip forming an acute angle; caudal process corneous, lamelliform, subtriangular, acute, and directed cephalodistad; central projection corneous, slender, triangular, and directed caudodistad.

Type locality.—"Sloughs along the Escambia River on State Highway 62, Escambia County, Florida"; holotype, USNM 81274.

Specimens examined.—I have examined only 46 specimens from Louisiana, all of which are from the Pearl River system as follows: St. Tammany parish: West Middle Pearl River, 7-1-39 (TU P-605); Pearl River, 2-11-38 (TU P-836); Talisheek Creek at Talisheek, various dates in February, March, June and August (TU 2877, 3040, 3041, 3056, 3059, 3093, 3180); 13 mi. n. Pearl River, 2-20-54 (TU 3107); Washington parish: Varnado, 3-29-53 (TU 3044); 5 mi. s. Varnado, 2-22-54 (TU 3057).

Life history.—With the Louisiana data added to those of Hobbs (1942) we have collections made in eight months (February through August, and October). Form I males were collected in March, May and June, and mature females only in February. Smallest juveniles (12 to 15 mm cephalothorax length) were collected in February only. Largest Louisiana specimens (cephalothorax length) are: ♂ I, 59 mm; ♂ II, 58 mm; ♀, 59 mm.

Ecological observations.—The 12 Louisiana collections have come from only six localities, and detailed habitat data were recorded on only two of these. All are from deep (i.e., over 36 inches) parts of creeks and rivers which are not easily sampled by ordinary methods. Perhaps this accounts for the small number of specimens collected to date. The creeks are small and fast-flowing, with sand and gravel bottoms and well-shaded banks. *P. bivittatus* was found particularly in the bottom debris where the current had scoured out large, deep holes. In Florida, Hobbs (1942) took the species from "both large and small, clear, sand bottomed creeks and from muddy sloughs. A few specimens were dug from simple burrows."

Distribution.—The Pearl River records of *P. bivittatus* represent a westward range extension of about 150 miles, with no records between the eastern and western limits. Probably this species will be found in the Pascagoula drainage and some of the other smaller coastal streams of Mississippi and Alabama.

PROCAMBARUS CLARKII (Girard)

Cambarus clarkii Girard, 1852, Proc. Acad. Nat. Sci. Phila. 6:91; *Cambarus clarkii clarkii* Girard, Faxon, 1914, Mem. Mus. Comp. Zool. 40:369; *Procambarus clarkii clarkii* (Girard) Hobbs, 1942, Amer. Midl. Nat. 28:342; *Procambarus clarkii* (Girard) Hobbs, 1942, Univ. Fla. Publ., Biol. Sci. Ser. 3(2):104.

Diagnosis.—Areola linear (obliterated). First pleopod of form I male reaching to middle of coxopodite of third pereiopod; apex with a distinct

shoulder on the cephalic surface and ending in four distinct parts: mesial process spiniform, extending distad only slightly beyond the other parts; cephalic process large, compressed, rounded cephalodistad but angular on the caudodistal margin; caudal process almost spatulate, making up the distal caudolateral portion of the appendage; central projection lying between and slightly mesiad of the cephalic and caudal processes (somewhat overhung by the cephalic process), entirely corneous, acute, and the least conspicuous of any of the four apical parts.

Type locality.—"Between San Antonio and El Paso del Norte, Texas"; types probably destroyed in the Chicago fire of 1871 according to Faxon (1914).

Specimens examined.—This crawfish is the commonest and economically the most important species in Louisiana. I have examined thousands of specimens. The vast majority of these had been cooked and were handled for only the few seconds necessary to shell and eat them, but a large number have also been analyzed more scientifically. Localities in 41 of the 64 parishes of the state are included in the material studied, as follows: Acadia, Ascension, Assumption, Calcasieu, Cameron (USNM, UMMZ, TU), DeSoto (USNM, TU), East Baton Rouge, Evangeline, Grant (USNM, TU), Iberia, Iberville (USNM, HHH, TU), Jefferson, Jefferson Davis (USNM), Lafayette, Lafourche (HHH, TU), Livingston (HHH, TU), Morehouse, Natchitoches (USNM, UMMZ, TU), Orleans (USNM, ANS, MCZ, TU), Ouachita, Plaquemines (HHH, TU), Pointe Coupee, Richland, Sabine, St. Bernard, St. Charles, St. James (HHH), St. John the Baptist, St. Landry, St. Martin, St. Mary, St. Tammany, Tangipahoa (USNM, TU), Tensas, Terrebonne (USNM, AMNH, MCZ, TU), Vermilion (UMMZ, TU), Washington, Webster and West Baton Rouge (HHH, TU).

Previously *P. clarkii* had been recorded from localities in twenty parishes: Ascension, Assumption, Calcasieu, Cameron, East Baton Rouge, Evangeline, Jefferson, Jefferson Davis, Lafourche, Livingston, Natchitoches, Orleans, Plaquemines, Pointe Coupee, St. Bernard, St. Charles, St. John the Baptist, St. Mary, St. Tammany, and Vermilion by Andrews (1906, 1907), Bick et al (1953), Cary (1906), Cary and Spaulding (1909), Ellis (1919), Gowanloch (1951), Hagen (1[illegible]), Ortmann (1905), Penn (1943, 1951, 1953b) and Viosca (1931, 195[illegible]).

Life history.—Many of the details of the life cycle have been studied. The following is a condensation taken from the contributions of Viosca (1939, 1953) and Penn (1943).

Winter: (1) Activity is restricted and most of the adults of both sexes pass the colder months in simple burrows in the drying marsh and swamp floors or their margins; (2) juveniles pass the winter in the water in or near the same localities, growing slightly; (3) in January, with the advent of the pre-spring rains, the burrowing adults enter the water and shortly thereafter the form II males change to form I (smallest male form I = 24 mm cephalothorax length).

Spring: (1) With returning warmth and an increase of plant food the juvenile population grows rapidly, most of them reaching sexual maturity by May; (2) some copulation occurs in late spring, but apparently many of the mature females retain sperm stored in their annuli the previous summer and early fall; (3) large numbers of maturing crawfishes are caught during this season and are enjoyed as a table delicacy by the people of southern Louisiana.

Summer: (1) The first eggs are laid and carried by the females in late June and early July (smallest known ovigerous female = 29 mm cephalothorax length); (2) succeeding waves of egg-laying continue through August and early September; (3) most, if not all, of the year old males are in form I during the summer; (4) copulation occurs frequently in July and continues through September; (5) females which will live through the coming winter molt after their young have become free-swimming; (6) the year's

crop of juveniles appears in water collections in increasingly larger numbers in late July and August; (7) the mature population disappears, many of the females apparently burrowing at this time.

Fall: (1) In September most of the form I males and a few of the mature females apparently are sexually exhausted and leave the marshes and swamps by the tens of thousands to participate in aimless overland wanderings; (2) most of these perambulating crawfishes fall prey to other animals, and the remainder certainly die as all of the "migrants" are in extremely poor physical condition; (3) the remaining adult females and large form II males burrow before the winter drought and cold sets in; (4) the juvenile population remains in the water.

Ecological observations.—An analysis of the 152 lots preserved in the Tulane collection would not account for the prodigious numbers of *P. clarkii* produced annually in marshes and swamps of the state. Collections in such places are usually made in the spring and seldom are preserved for scientific purposes, (even by the writer!). Accordingly, the figures below on habitat utilization are weighted according to my personal observations and knowledge of the species.

Habitat	Estimate of Percent of Population Utilizing each Habitat
Marshes and marsh pools	35
Swamps and swamp pools	30
Lakes, ponds, borrow pits	14
Ditches (mostly roadside)	12
Slow-flowing streams (mostly bayous)	8
Pineland sloughs and springs	1

An analysis of the various physical and biological factors in all habitats may be summarized in the statement that *P. clarkii* occurs most frequently (and in greatest abundance) in shallow water (i.e., less than 15 inches deep) which is either clear or muddy, permanent, static, and exposed to full sunlight. The few pH readings indicate water close to neutral, the range being between 5.6 and 7.2. Most of the collections are found in habitats with mud bottoms and with aquatic vegetation abundant. The aquatic plants most commonly found in these places, in order of frequency of occurrence, are *Scirpus* spp., *Typha* spp., *Achyranthes philoxeroides, Eichhornia crassipes, Jussiaea* spp., *Polygonum* spp., *Pontederia* spp., *Sagittaria* spp., *Lemna* spp., *Azolla caroliniana, Myriophyllum* spp., *Cabomba* sp., *Ceratophyllum* spp., *Eleocharis* spp., *Juncus* spp., *Bramia* sp., *Zizaniopsis miliacea, Hydrocotyl* sp. and *Najas* sp. In connection with the plants it is interesting to note that Viosca (1931) and Martin and Uhler (1939) recorded *P. clarkii* feeding on *Achyranthes, Jussiaea, Polygonum, Sagittaria, Najas, Chara, Elodea, Potamogeton* and algae, but not on *Myriophyllum* and *Marsilea.*

A number of collections of *P. clarkii* have been made in slightly brackish marshes and along the shore of Lake Pontchartrain where salinity ranged as high as 6 ‰. In this connection it is worth noting that Helff (1929, 1931) using mature specimens and Steeg (1942) using juveniles demonstrated that *P. clarkii* can survive laboratory tests for a week in 1.17 and 1.5 percent solutions (11.7 and 15.0 ‰) of NaCl respectively, but are killed in significant numbers by stronger NaCl solutions.

Viosca (1950) noted that *P. clarkii* attains greater size in the five-foot-deep

waters of the swamps of the Morganza Floodway (Atchafalaya River) near Pierre Part, Assumption Parish, La., where they are caught in baited wire-frame cone-traps for commercial uses. Here the crawfish average eight to the pound as compared with the more usual 12 to 20 to the pound for individuals taken in the shallower marshes and swamps. The phenomenal productivity of a marsh near Lafitte, Jefferson Parish, La., as noted by Gowanloch (1951) is more or less typical of such favorable habitats throughout southern Louisiana. In a small section of this marsh (area not known) three men using ten to fifteen baited crawfish nets each caught 22 sacks (=approximately 2,400 pounds) of this species in one eight-hour day.

Color variation.—The normal color of mature *P. clarkii* is deep red; in some individuals this is so dark as to appear almost black. Several years ago attention was called to the occurrence of blue specimens of this crawfish from two points on the east (Orleans parish) and west (St. Charles parish) outskirts of New Orleans (Penn, 1951). In the last two years seafood dealers have reported increasing numbers of blue specimens from additional localities in Assumption parish. The genetic basis for the survival and increase of this assumed mutation is being investigated.

PROCAMBARUS PLANIROSTRIS Penn

Procambarus planirostris Penn, 1953, Tulane Stud. Zool. 1(6):71.

Diagnosis.—Rostrum without lateral spines; areola narrow. First pleopod of form I male reaching to cephalic side of coxopodite of third pereiopod. Apex terminating in four parts which together extend caudad at about a 40° angle to the shaft of the pleopod; mesial process non-corneous, spiniform, directed caudodistad, and not extending beyond the other terminal elements; cephalic process corneous, arising on mesial side of central projection, directed caudodistad, excavate on caudolateral surface, and closely applied to the central projection; central projection corneous, compressed, "beak-like" in shape, with apex directed caudad; caudal process consisting of two corneous parts: mesially a low, longitudinal ridge flanked by a leaf-like element which extends distally, its apex coming in contact with the overhanging central projection. Cephalic margin of the shaft of the pleopod with a distinct shoulder.

Type locality.—"One mile south of Walker (on La. hwy. 336), Livingston Parish, La."; holotype: USNM 95674.

Specimens examined.—I have seen only 29 specimens from Louisiana, all of which were included in the paratypic series. These were from East Baton Rouge, Livingston, St. Tammany and Washington parishes. Hobbs (pers. com.) has material from two additional Louisiana localities: Livingston parish: 2.9 mi. w. Albany, 4-17-54 (HHH); Tangipahoa parish: 3.5 mi. wsw. St. Tammany-Tangipahoa parish line, 4-17-54 (HHH).

Life history.—Form I males have been collected in February, March and July and mature females in January, February, March and August. The smallest juveniles (7 to 10 mm cephalothorax length) were collected in January and February which suggests that egg-laying occurs in early winter (November-December); ovigerous females are unknown.

Ecological observations.—The greatest numbers of individuals were taken from burrows and surface water in a low area of mixed hardwood, pine and

palmetto flatwoods, however a few individuals have also been collected in such diverse habitats as creeks, a swamp, roadside ditches and a pond. The physical and biological factors affecting these habitats may be summarized as shaded (86%), temporary situations (55%), clear or turbid water (50% each), static water (71%), mud or clay bottom (87%), less than 15 inches deep (80%), with aquatic vegetation present (55%). Tentatively, this species may be classed as a secondary burrower in Hobbs' (1942) categories.

SPICULIFER GROUP

Diagnosis.—Rostrum with a well-developed spine along either margin and terminating in a long acumen; areola wide and much shorter than cephalic section of the cephalothorax; two conspicuous lateral spines present on either side of the cephalothorax. First pleopod of form I male terminates in four parts: mesial process spiculiform and always prominent; cephalic process relatively small and in apposition with and partially hooding the central projection; central projection conspicuously corneous and making up the bulk of the terminal part of the pleopod; caudal process arises from the base of and caudolaterad of the central projection and is the least conspicuous of the four terminal processes (after Hobbs, 1942).

Four species of this group occur in Louisiana.

PROCAMBARUS VIOSCAI Penn

Procambarus vioscai Penn, 1946, J. Wash. Acad. Sci. 35:27.

Diagnosis.—First pleopod of form I male reaching to middle of coxopodite of third pereopod and terminating in four parts: mesial process spiculiform, directed caudodistad and laterad; cephalic process corneous, lying cephalolaterad of the central projection, flattened on lateral face and slightly excavate on mesial face; caudal element consisting of three parts, a) caudal knob in lateral aspect a low, rounded knob, non-corneous, b) caudal process corneous, small and subacute, and c) accessory process reduced, extending as a low corneous ridge across the mesial face of the central projection; central projection corneous, blunt-tipped.

Type locality.—"Big Creek at Fishville, about 3 miles east of Pollock, Grant Parish, La."; holotype: USNM 79925.

Specimens examined.—From Louisiana I have seen 967 specimens from 68 localities in Caldwell, Catahoula, East Baton Rouge, East Feliciana, Grant (USNM, AMNH, HHH, ASMNH, TU), Jackson, LaSalle, Lincoln, Livingston, Ouachita (HHH, TU), Rapides (USNM, TU), St. Helena, St. Tammany, Tangipahoa, Union, West Feliciana and Winn parishes. Previously *P. vioscai* has been reported from Grant (Penn, 1946), Ouachita (Penn, 1946) and St. Tammany parishes (Bick et al, 1953).

Life history.—A few tentative statements may be made from an analysis of the seasonal distribution of size groups of the Louisiana specimens which have been examined.

There is a significant increase in the number of small juveniles (5 to 14 mm cephalothorax length) in July which is suggestive that the major egg-laying period occurs in early summer (May through July). This is corroborated by the collection of one ovigerous female and another carrying young in late May

and one ovigerous female in late June in the northern part of the state (Lincoln and Union parishes respectively). A second increase in small juveniles which occurs in the spring (March and April) is suggestive of another period of egg-laying in the late winter (January-February) or possibly earlier, assuming that the juveniles would not grow rapidly during the colder months. There is no corroboration for this latter premise as collections are not adequate for the late fall and winter months (October-February). Larger juveniles (15 to 25 mm cephalothorax length) occur in large numbers only in the spring (March-May).

Form I males have been collected from March through August and in November, but were most abundant in early summer (May-July). Females bearing sperm plugs in their annuli have been collected from March through August, but were most abundant in July. The smallest form I males and females with plugged annuli were 23 mm cephalothorax length.

Ecological observations.—An analysis of 46 lots is summarized briefly in the following table.

Habitat	Percent of Total Collections
Flowing creeks	88
Springs	3
Pools in dry creek beds, or alongside creeks	3
Swamps	3
Lake (impounded creek)	1.5
Ditch (field)	1.5

The various physical and biological factors in all habitats combined may be summarized in the statement that *P. vioscai* occurs most frequently in shallow water, i.e. less than 18 inches deep (68%), which is clear (71%), permanent (92%), flowing (91%) and shaded (62%). Most collections were from habitats with sand bottoms (87%) and with no or sparse aquatic vegetation (83%). Aquatic plants which were recorded were *Vallisneria* sp., *Elodea* sp., *Sparganium* sp., *Myriophyllum* sp., *Bramia* sp., and *Typha* sp.

PROCAMBARUS PENNI Hobbs

Procambarus penni Hobbs, 1951, J. Wash. Acad. Sci. 41:273.

Diagnosis.—First pleopod of form I male reaching to cephalic side of coxopodites of third pereiopods, and terminating in four parts: mesial process spiculiform and directed caudodistad; cephalic process subacute and extending slightly cephalomesiad; caudal element consisting of three parts, a) caudal knob acute and noncorneous, b) caudal process slender, sublanceolate and excavate caudad, and c) accessory process extends across the proximocaudal face of the caudal process and central projection as a thin corneous ridge; central projection corneous and truncate distad.

Type locality.—"Talisheek Creek at Talisheek, St. Tammany Parish, La."; holotype: USNM 91662.

Specimens examined.—From Louisiana I have examined 629 specimens, all from tributaries of the Pearl River in St. Tammany and Washington parishes.

Life history.—From an analysis of the Louisiana material in the Tulane collection it appears that the seasonal cycle of *P. penni* closely parallels that of *P. vioscai.*

An increase in the number of small juveniles (6 to 14 mm cephalothorax length) in July is suggestive that the major egg-laying period occurs in spring and early summer (April through June). In corroboration of this, one ovigerous female was collected in April at the type locality. A second increase in small juveniles occurs also in late December and January which is suggestive of a second spawning period in late fall (October-November). Larger juveniles (15 to 25 mm cephalothorax length) occur in greatest numbers at two times during the year also: early spring (February-March) representing perhaps the maturing early winter small juveniles; and early fall (September-October) representing perhaps the maturing summer small juveniles. An increase in the number of form II males from December through March is followed by a similar increase of form I males from January through April. The number of females bearing sperm plugs in their annuli increases from March through May, and again from October through December. This is suggestive of two definite copulation periods—one in the spring preceding the summer egg-laying, and the other in the early fall preceding the late fall egg-laying.

Form I males have been collected in all months except August and September. Females with sperm plugs have been collected only in March, April, May, October, November and December. The smallest form I male = 23 mm cephalothorax length; the smallest female with a sperm plug = 24 mm cephalothorax length.

Ecological observations.—Forty-eight lots of *P. penni* yield the following information. Habitats: Flowing creeks (95%), a spring (2.5%), and an overflow pond beside a creek (2.5%). Physical and biological factors affecting all habitats: Permanent (98%), shaded (73%), clear water (83%), flowing (98%), over 18 inches deep (84%), with aquatic vegetation present (74%), and with sand, gravel, or sand-and-gravel bottoms (71%). Aquatic plants recorded in these habitats were *Sparganium* sp., *Potamogeton* sp., *Ceratophyllum* sp., and *Achyranthes philoxeroides.*

PROCAMBARUS NATCHITOCHAE Penn

Procambarus natchitochae Penn, 1953, Amer. Mus. Novitates, No. 1636:5.

Diagnosis.—First pleopod of form I male reaching to cephalic side of coxopodite of third pereiopod, and terminating in four parts: 1) mesial process spiculiform and directed laterodistad; 2) cephalic process corneous, acute, excavate caudad and extending straight distad; 3) caudal element consisting of three parts: a) caudal knob in lateral aspect subacute and noncorneous, b) caudal process corneous, subacute, and directed mesiodistad, and c) accessory process forming a thin transverse, corneous ridge caudad of the central projection; 4) central projection corneous, truncate and somewhat beaked distad.

Type locality.—"Tributary of Spring Creek at Melder (on La. hwy. 85), Rapides parish, La."; holotype: USNM 93649.

Specimens examined.—I have seen 364 specimens of *P. natchitochae,* over half of which were included in the paratypic series from Claiborne, Natchitoches, Rapides, Vernon and Webster parishes in Louisiana, and Columbia county, Arkansas.

Additional specimens have since been collected from ten localities in Bossier, DeSoto, Natchitoches, Rapides and Webster parishes, Louisiana.

Life history.—We have collections from only seven months: February through August. Form I males are present in April, May, June and August; mature females only in March, April, May and June. Of the April and May females 35 percent have sperm plugs in their annuli; none of the others bear sperm plugs. Small juveniles (9 to 14 mm cephalothorax length) occurred only in the April collections.

Ecological observations.—Seventeen lots of *P. natchitochae* indicate the habitat to be creeks (100%), which are permanent (100%) and flowing (93%). Other factors affecting these habitats were: water over 18 inches deep (80%), shaded (58%), either clear or turbid water (50% each). Most of the collections were from creeks with sand or sand-and-gravel bottoms (70%) and with little or no aquatic vegetation present (90%).

PROCAMBARUS DUPRATZI Penn

Procambarus dupratzi Penn, 1953, Amer. Mus. Novitates, No. 1636:1.

Diagnosis.—First pleopod of form I male reaching to middle of coxopodite of third pereiopod, and terminating in four parts which as a unit extend caudad at about a 40° angle to the shaft of the pleopod: Mesial process spiculiform, basal two-thirds directed caudodistad at about a 45° angle, apical third bent so that it extends straight caudad; cephalic process corneous, subacute, excavate caudad and directed caudodistad; caudal element consists of three parts, a) caudal knob in lateral aspect inconspicuous, subacute, noncorneous, b) caudal process corneous, acute and directed caudomesiad, and c) accessory process corneous, forming an inconspicuous, thin, transverse ridge caudad of the central projection; central projection corneous, subacute, directed caudodistad.

Type locality.—"Attoyac Bayou, 5.6 miles southwest of Timpson (on U. S. hwy. 59), Shelby County, Texas"; holotype: USNM 93652.

Specimens examined.—I have seen only 131 specimens of *P. dupratzi*, most of which were included in the paratypic series from tributaries of the Sabine River in Sabine and Vernon parishes in Louisiana in addition to tributaries of the Sabine, Neches and Trinity rivers in Anderson, Nacogdoches, Panola and Shelby counties in Texas.

Additional material has been collected from Louisiana as follows: *Sabine parish*: Phillip's Creek, 5.6 mi. sw. Ft. Jesup, 4-11-53 (TU 2920); *Vernon parish*: Bayou Castor, 2.3 mi. e. Leesville, 4-11-53 (TU 2923); tributary of Calcasieu River, 11 mi. e. Leesville, 4-11-53 (TU 2925).

Life history.—Collections have been made in only four months: April, June, August and November. Form I males are present in April, June and August; mature females only in April, but 16 percent of these had sperm plugs in their annuli. Small juveniles (8 to 14 mm cephalothorax length) occurred in large numbers both in mid-April and late August which suggests that both spring and early winter spawning periods are used.

Ecological observations.—Fourteen Louisiana lots are available for analysis. Apparently *P. dupratzi* is confined to permanently flowing creeks (100%), in which the water is more than 18 inches deep (71%), clear or turbid (50%

each), and shaded (64%). Most of the collections were from creeks with sand or sand-and-mud bottoms (31% each) and with little or no aquatic vegetation (90%). The only aquatic plant recorded was *Potamogeton* sp.

HINEI SECTION

This monotypic section was designated to receive the disjunct *P. hinei* which occurs only in Louisiana and eastern Texas (Penn, 1953b). Its diagnosis is that of the species.

PROCAMBARUS HINEI (Ortmann)

Cambarus (*Cambarus*) *hinei* Ortmann, 1905, Ohio Nat. 6:401; *Procambarus hinei* (Ortmann) Hobbs, 1942, Amer. Midl. Nat. 28:342; *Procambarus hinei* (Ortmann) Penn, 1953, Tulane Stud. Zool. 1(5):63.

Diagnosis.—Rostrum tapering sharply, with slight indication of lateral spines; areola wide; without lateral spines on cephalothorax (or, only a single small one on each side in some specimens); chela subcylindrical, palm longer than fingers. First pleopod of form I male reaching to coxopodite of third pereiopod, and terminating in three parts: mesial process noncorneous, spiculiform and extending laterodistad; cephalic process corneous, lying near to and mesiocaudad of the mesial process, truncate near apex, and directed laterodistad; caudal process not developed; central projection corneous, acute and somewhat compressed. A shoulderlike hump is present on the cephalomesial part of the apex of the pleopod.

Type locality.—"One quarter mile from Gulf Beach, near Cameron, Cameron parish, La."; types reported as unknown by Penn (1953b) but since then found in the Ohio State Museum, Columbus, Ohio (no catalog number).

Specimens examined.—This species is usually common where it occurs, but its distribution is quite spotty within its range. I have examined 314 specimens from 23 localities in Ascension, Calcasieu, Cameron (USNM, HHH, TU), Franklin, Iberville, Morehouse, Ouachita, Pointe Coupee (HHH, TU), St. Landry, Terrebonne (USNM, TU), Vermilion and West Baton Rouge parishes. Previously it had been recorded from Cameron parish only by Ortmann (1905), Cary (1906), Cary and Spaulding (1909) and Penn (1953b).

Apparently *P. hinei* is restricted to the Quarternary lowlands of Louisiana west of the Mississippi valley and southeastern Texas. Within this area it has been found only in the subdivisions described by Holland (1944) as the Prairie Terrace, Arkansas Alluvial Cone, lower Mississippi Alluvial Plain and Deltaic Plain units. The first of these is the youngest of four Pleistocene terraces and the other three are all Recent floodplain or deltaic in origin. Such a distributional pattern is suggestive that *P. hinei* split off from its parental stock and became a distinct species in mid- or late-Pleistocene.

Life history.—No collections have been made in late summer and early fall (August through November). One female carrying young was collected on February 29th in central Louisiana (Pointe Coupee parish) and two ovigerous females have been obtained from commercial collectors in the southeastern part of the state (Terrebonne parish). These latter were taken presumably in March or April which is the season for catching marketable *P. clarkii* with

which they were found. The February 29th female had 69 young which averaged 2 mm cephalothorax length. Large numbers of small juveniles (6 to 10 mm cephalothorax length) have been collected only in March and April. Females bearing sperm plugs in their annuli were most abundant in February, although a few have been found also in April and December. Both form I and II males were most abundant in April and July; mature females were most numerous in April. Smallest form I male = 11 mm cephalothorax length; smallest female with a sperm plug in her annulus ventralis = 12 mm cephalothorax length.

Ecological observations.—An analysis of 21 lots shows the commonest habitat to be semipermanent ponds, borrow pits and ditches (67%); other habitats are swamps and swamp ponds (14%), shallow bayous (9%), marshes (5%) and sloughs (5%). Physical and biological factors affecting these habitats were: Exposed to sunlight (78%), semipermanent situations (67%), clear or turbid water (50% each), static water (94%), mud bottoms (100%), water less than 15 inches deep (89%), and with sparse aquatic vegetation (77%). Aquatic plants found were *Polygonum* spp., *Potamogeton* spp., and *Myriophyllum* spp. pH readings ranged from 6.5 to 7.0.

A slightly brackish content to the water seemed to be favorable in the vicinity of Hackberry, Cameron parish, La. Two small ponds devoid of aquatic vegetation which were teeming with *P. hinei* had salinities of 0.63 and 0.38 ‰ respectively. Freshwater ponds in the same general area in which pondweed (*Potamogeton* sp.) thrived contained few *P. hinei.* The animal's habit of roiling the water may discourage other species of crawfishes as well as aquatic plants, for it is never found in abundance with other crawfish species.

BARBATUS SECTION

Diagnosis.—Cephalodistal surface of the first pleopod of form I male terminates in a ridge (sharp or truncate) or a knob-like prominence which is distinctly not a part of one of the terminal processes; mesial process always directed distad unless spatulate; cephalic process when present always extends distad from mesial surface; central projection never decidedly the most conspicuous element. Hooks present on ischiopodites of third, or third and fourth pereiopods (after Hobbs, 1942).

The *Barbatus* section is divided into several groups, of which only the *simulans* group is represented in Louisiana.

SIMULANS GROUP

Diagnosis.—Male with hooks on third pereiopods only. Areola rather narrow or obliterated; rostrum without lateral spines. First pleopod of form I male terminating in four parts: mesial process elongate, extending distad beyond apex of all other terminal parts; central projection somewhat saber-shaped and shorter than mesial process; cephalic process short, usually acute and situated caudad of cephalic margin of pleopod; caudal element consisting of a caudal knob capped by an irregularly-leaflike caudal process.

Two closely related species are found in Louisiana.

PROCAMBARUS SIMULANS SIMULANS (Faxon)

Cambarus simulans Faxon, 1884, Proc. Amer. Acad. Arts & Sci. 20:112; *Cambarus gallinus* Cockerell & Porter, 1900, Proc. Acad. Nat. Sci. Phila. 52:434; *Cambarus baumgartneri* Harris (nomen nudum), 1901, Trans. Kans. Acad. Sci. 17:115; *Procambarus simulans* (Faxon) Hobbs, 1942, Amer. Midl. Nat. 28:342; *Procambarus simulans simulans* (Faxon) Villalobos, 1954, An. Inst. Biol. Mex. 25:289.

Diagnosis.—First pleopods of form I male reaching to cephalic margin of third pereiopod and terminating in four parts: 1) mesial process elongate, spiculiform, somewhat compressed proximad; 2) cephalic process directly cephalad of mesial process and mesad of central projection, acute, less than half the length of the mesial process; 3) caudal element consisting of an angulate caudal knob capped laterodistad by the caudal process which extends as a distal oblique (cephalomesad to caudolaterad) corneous ridge; 4) central projection corneous, acute and extending somewhat cephalolaterad.

Type locality.—"Dallas, Dallas County, Texas"; holotype: MCZ 3646.

Specimens examined.—The subspecies was provisionally recorded from Louisiana in 1941 and later definitely reported from the Sabine watershed by Penn (1941, 1953d). One-hundred sixteen specimens have been examined from the Sabine, Red, Calcasieu and Bayou Teche river systems in western Louisiana as follows: Allen parish: Elizabeth (TU 1057); Beauregard parish: 3 mi. n. Newlin (TU P-354); Bossier parish: 7 mi. w. Plain Dealing (TU 424); 4 mi. ne. Plain Dealing (TU 1422); DeSoto parish: Naborton (TU 1439); Natchitoches parish: 3.6 mi. e. Cloutierville (TU 75); Ajax (TU 1279); 4 mi. s. Derry (TU 1365); tributary to Red river, 1.8 mi. e. Provencal (TU 2909); Rapides parish: 3.6 mi. w. Lecompte (TU 2676); Sabine parish: 4.4 mi. nw. Noble (TU 2860); 5.6 mi. sw. Ft. Jesup (TU 2920); 4.4 mi. s. Florien (TU 2921); Vernon parish: 3.2 mi. nw. Anacoco (TU 2762); tributary to Calcasieu river, 11 mi. e. Leesville (TU 2925).

Life history.—The occurrence of small juveniles in February and April is indicative of egg-laying in January and February. Form I males were taken in April and August; mature females only in April. Ovigerous females have not been recorded in Louisiana, but have been reported from burrows in May in southern Nevada (Harris, 1903), in August in south-central Kansas (Harris, 1902) and in early September in Oklahoma (Creaser and Ortenburger, 1933); females carrying young were found in late April in Kansas (Williams and Leonard, 1952).

Ecological observations.—An analysis of 12 lots from Louisiana yields the following. The largest number of specimens was taken from creeks (58%). Other habitats were: Ditches (25%), potholes in dry creek beds (8%), and pineland sloughs (8%). The various physical and biological factors affecting these habitats were: Shaded (58%), permanent situations (73%), turbid water (60%), flowing water (66%), sand-and-mud bottoms (60%), water less than 15 inches deep (64%), and without aquatic vegetation (60%).

These observations are at variance with those of Williams and Leonard (1952) who report *P. s. simulans* as "not common in Kansas streams" and indicate that it is typically a burrowing form in that part of its range. On the other hand, my observations somewhat parallel those of Creaser and Ortenburger (1933) who state that in Oklahoma *simulans* is "particularly fond of muddy streams and ponds" and is "not essentially a burrowing species."

PROCAMBARUS TULANEI Penn

Procambarus tulanei Penn, 1953, J. Wash. Acad. Sci. 43:163.

Diagnosis.—First pleopod of form I male extending to the cephalic side of the coxopodite of third pereiopod, and terminating in four parts: 1) mesial process elongate, flattened on its transverse axis, extending slightly laterocaudad; 2) cephalic process subacute, a little less than half the length of mesial process, directed slightly cephalomesiad; 3) caudal element consisting of a straight, elongate caudal knob capped distally by the corneous caudal process which is irregularly-leaflike and excavate on its caudal face; 4) central projection corneous, saber-shaped and directed slightly caudomesiad.

Type locality.—"A small unnamed tributary of Bayou d'Arbonne, 4 mi. w. of Dubach, Lincoln Parish, Louisiana"; holotype: USNM 93655.

Specimens examined.—I have seen only 170 specimens from Louisiana, most of which were included in the paratypic series, from tributaries of the Ouachita and Red rivers in Caldwell, Grant, Jackson and Lincoln parishes. In addition, material has been collected from: Caldwell: near Kelly, 3-21-53, 2-10-54 (TU 2875, 3001, 3002, 3003); Jackson: 2.4 mi. w. Quitman, 6-2-55 (TU 3155); Lincoln: Ruston, various dates in February, April and May (TU 3185-3189); Natchitoches: 5.9 mi. n. Chestnut, 6-2-55 (TU 3156): Winn: 2 mi. s. Hudson, 4-5-53 (TU 2892).

Life history.—All of the form I males have been taken in February and April only, and ovigerous females are unknown, however, an analysis of the size groups in all collections yields some information. The presence of form I males in early spring only indicates that copulation probably occurs at that time, and the large numbers of small juveniles (8 to 12 mm cephalothorax length) in February is indicative of simultaneous egg-laying. It is probable that the females retire to burrows before laying eggs as all except two of the mature specimens have been taken from burrows. On the other hand, all except one of the juveniles were taken in open water.

Juveniles less than 20 mm cephalothorax length possess either small lateral spines or small humps on the rostrum at the base of the acumen, and a small lateral spine on either side of the cephalothorax. Slightly larger juveniles (up to 30 mm cephalothorax length) may have reduced lateral spines on the cephalothorax, and bear only reduced humps on the rostrum. Larger specimens lack these features entirely.

Ecological observations.—Apparently *P. tulanei* is a secondary burrower as all except two of the mature specimens were taken from burrows. The burrows may or may not have chimneys; when present, the chimneys are about twelve inches high, well-constructed, six to eight inches in diameter at the base, and four inches in diameter at the top, with the opening about two inches across. The burrows may be simple, or with branches near the terminus; the deepest one excavated had the terminal chamber five feet below the surface of the ground. Most of the burrows observed have been in the banks of streams and ditches, although one was located about 30 yards from the edge of a stream.

With only one exception all juveniles have been taken from the water of flowing creeks (83%) or borrow pits (17%). Physical and biological factors affecting these juvenile habitats were: Shaded (66%), semipermanent situations (80%), clear water (80%), with clay or mud bottoms (83%), shallow or deep water (50% each), and without aquatic vegetation (83%).

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A List of Nematode Parasites from California Mammals

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This report summarizes published and unpublished information on the occurrence and distribution of adult nematode parasites in wild mammals in California. It illustrates the sketchiness of our knowledge concerning parasitic helminths and their occurrence in economically unimportant host species, and it reflects the increasing attention directed toward the study of parasites of game animals, such as deer.

With few exceptions, the common names of the hosts, as given in the host list, were obtained from Burt and Grossenheider (1952). In the parasite list, new locality records within the state, as well as first reports for the state, are indicated by an asterisk after the locality in question.

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List of Parasites According to Hosts

Marsupialia

Didelphis virginiana, Virginia Opossum.—*Physaloptera turgida* (Rudolphi, 1819).

Chiroptera

Macrotus californicus, Leafnose Bat.—*Glyptostrongylus collaris* Neyland, 1955.
Tadarida mexicana, Mexican Freetail Bat.—*Molinostrongylus delicatus* (Schwartz, 1927).
Antrozous pallidus, Pallid Bat.—*Allintoshius* sp.

Rodentia

Citellus beecheyi, California Ground Squirrel.—*Trichuris citelli* Chandler, 1945; *Ascaris columnaris* Leidy, 1856*; *Syphacia* sp.

C. nelsoni, San Joaquin Antelope Squirrel.—*Physaloptera* sp.

Dipodomys merriami, Merriam Kangaroo Rat.—*Mastophorus dipodomis* Read and Millemann, 1953; *Trypanoxyuris deserti* Read and Millemann, 1953; *Rictularia dipodomis* Tiner, 1948; *Gongylonema neoplasticum* Fibiger and Ditlevsen, 1914.

D. panamintinus, Panamint Kangaroo Rat.—*Mastophorus dipodomis* Read and Millemann, 1953; *Trypanoxyuris deserti* Read and Millemann, 1953; *Rictularia dipodomis* Tiner, 1948; *Gongylonema neoplasticum* Fibiger and Ditlevsen, 1914.

D. morroensis, Morro Bay Kangaroo Rat.—*Trypanoxyuris deserti* Read and Millemann, 1953; *Rictularia dipodomis* Tiner, 1948.

* Probably a variant of *Ascaris laevis* Leidy, 1856 (see Tiner, 1951).

D. deserti, Desert Kangaroo Rat.—*Mastophorus dipodomis* Read and Millemann, 1953.

Perognathus californicus, California Pocket Mouse.—*Trichuris perognathi* Chandler, 1945.

P. sp.—*Mastophorus dipodomis* Read and Millemann, 1953.

Thomomys bottae, Valley Pocket Gopher.—*Trichuris fossor* Hall, 1916.

Peromyscus californicus, California Mouse.—*Trichuris peromysci* Chandler, 1946.

P. boylei, Brush Mouse.—*Heligmosomum* sp.

Neotoma fuscipes, Dusky-footed Woodrat.—*Nematodirus tortuosus* Tucker, 1942; *Trichuris neotomae* Chandler, 1945; *Heligmosomoides* sp.

N. lepida, Desert Woodrat.—*Nematodirus tortuosus* Tucker, 1942.

Rattus norvegicus, Norway Rat.— *Physaloptera maxillaris* Molin, 1860.

Mus musculus, House Mouse.—*Nematospiroides dubius* Baylis, 1926.

LAGOMORPHA

Sylvilagus audubonii, Desert Cottontail.—*Obeliscoides cuniculi* (Graybill, 1923); *Nematodirus leporis* Chandler, 1924; *Passalurus ambiguus* (Rudolphi, 1819); *Dermatoxys veligera* (Rudolphi, 1819).

Ochotona princeps, Pika.—*Cephaluris coloradensis* Olsen, 1949; *Labiostomum naimi* Akhtar, 1941; *Dermatoxys* sp.

CETACEA

Phocoena phocoena, Harbor Porpoise.—*Pharurus convolutus* (Kuhn, 1829); *Halocercus invaginatus* (Quekett, 1841); *Stenurus vagans* (Eschricht, 1841). *Phocoenoides dalli*, Dall Porpoise.—*Halocercus kirbyi* Dougherty, 1944.

CARNIVORA

Mephitis mephitis, Striped Skunk.—*Physaloptera maxillaris* Molin, 1860; *Crenosoma mephitidis* Hobmaier, 1941; *Angiocaulus gubernaculatus* (Dougherty, 1946).

Spilogale gracilis, Spotted Skunk.—*Crenosoma mephitidis* Hobmaier, 1941.

Taxidea taxus, Badger.—*Physaloptera torquata* Leidy, 1886; *Angiocaulus gubernaculatus* (Dougherty, 1946).*

Procyon lotor, Raccoon.—*Ascaris columnaris* Leidy, 1856; *Crenosoma goblei* Dougherty, 1945.

Urocyon cinereoargenteus, Grey Fox.—*Physaloptera rara* Hall and Wigdor, 1918.

Canis latrans, Coyote.—*Thelazia californiensis* Price, 1930.

Lynx rufus, Bobcat.—*Metathelazia californica* Skinker, 1931.

Ursus americanus, Black Bear.—*Trichinella spiralis* (Owen, 1835); *Thelazia californiensis* Price, 1930.

PINNIPEDIA

Zalophus californianus, California Sea Lion.—*Parafilaroides decorus* Dougherty and Herman, 1947.

Eumetopias jubata, Stellar Sea Lion.—*Parafilaroides nanus* Dougherty and Herman, 1947; *P. prolificus* Dougherty and Herman, 1947; *P.* sp.

ARTIODACTYLA

Odocoileus hemionus, Mule Deer.—*Strongyloides papillosus* (Wedl, 1856); *Oesophagostomum venulosum* (Rudolphi, 1809); *Chabertia ovina* (Fabricius, 1788); *Trichostrongylus colubriformis* (Giles, 1892); *T. axei* (Cobbold, 1879); *T. vitrinus* Looss,

* Synonym: *Angiostrongylus gubernaculatus* (see Skrjabin, 1952).

1905; *Haemonchus contortus* (Rudolphi, 1803); *Ostertagia circumcincta* (Stadelmann, 1894); *O. trifurcata* (Ransom, 1907); *Nematodirus filicollis* (Rudolphi, 1802); *N. spathiger* (Railliet, 1896); *Dictyocaulus filaria* (Rudolphi, 1809); *D. viviparus* (Bloch, 1782); *D. hadweni* (Chapin, 1925); *Parelaphostrongylus odocoilei* (Hobmaier and Hobmaier, 1934); *Thelazia californiensis* Price, 1930; *Trichuris ovis* (Abilgaard, 1795); *T.* sp.; *Setaria cervi* (Rudolphi, 1819); *S. labiato-papillosa* (Alessandrini, 1838); *Wehrdikmansia cervipedis* (Wehr and Dikmans, 1935); *Elaeophora schneideri* Wehr and Dikmans, 1935.

Parasite List

ASCARIDAE

Ascaris columnaris.—Citellus beecheyi. Hastings Reservation, Monterey County, (Linsdale, 1946); *Procyon lotor.* Hastings Reservation, Monterey County.*

OXYURIDAE

Passalurus ambiguus.—Sylvilagus audubonii. San Joaquin Experimental Range, Madera County, (Herman and Jankiewicz, 1943).

Dermatoxys veligera.—Sylvilagus audubonii. San Joaquin Experimental Range, Madera County, (Herman and Jankiewicz, 1943).

Trypanoxyuris deserti.—Dipodomys merriami. Palmdale and Victorville, San Bernardino County, (Read and Millemann, 1953); *D. panamintinus.* Palmdale and Victorville, San Bernardino County, (Read and Millemann, 1953); *D. morroensis.* Morro Bay (Read and Millemann, 1953).

Cephaluris coloradensis.—Ochotona princeps. Bodie, Mono County, (Severaid, 1955).

Labiostomum naimi.—Ochotona princeps. Bodie, Mono County, (Severaid, 1953).

Dermatoxys sp.—*Ochotona princeps.* Bodie, Mono County, (Severaid, 1955).

Syphacia sp.—*Citellus beecheyi.* Hastings Reservation, Monterey County, (Linsdale, 1946).

RHABDITIDAE

Strongyloides papillosus.—Odocoileus hemionus. Hopland Field Station, Mendocino County, (Longhurst and Douglas, 1953).

STRONGYLIDAE

Oesophagostomum venulosum.—Odocoileus hemionus. Hopland Field Station, Mendocino County, (Longhurst and Douglas, 1953).

Chabertia ovina.—Odocoileus hemionus. Hopland Field Station, Mendocino County, (Longhurst and Douglas, 1953).

TRICHOSTRONGYLIDAE

Trichostrongylus colubriformis.—Odocoileus hemionus. Hopland Field Station, Mendocino County, (Longhurst and Douglas, 1953).

T. axei.—Odocoileus hemionus. Hopland Field Station, Mendocino County, (Longhurst and Douglas, 1953).

T. vitrinus.—Odocoileus hemionus. Hopland Field Station, Mendocino County, (Longhurst and Douglas, 1953).

Obeliscoides cuniculi.—Sylvilagus audubonii. San Joaquin Experimental Range, Madera County, (Herman and Jankiewicz, 1943).

Ostertagia circumcincta.—Odocoileus hemionus. Hopland Field Station, Mendocino County, (Longhurst and Douglas, 1953).

O. trifurcata.—Odocoileus hemionus. Hopland Field Station, Mendocino County, (Longhurst and Douglas, 1953).

Haemonchus contortus.—Odocoileus hemionus. Hopland Field Station, Mendocino County, (Longhurst and Douglas, 1953).

Nematodirus tortuosus.—Neotoma fuscipes. West Los Angeles, (Tucker, 1942), and Hastings Reservation, Monterey County (Linsdale and Tevis, 1951); *N. lepida.* West Los Angeles, (Tucker, 1942).

N. leporis.—Sylvilagus audubonii. San Joaquin Experimental Range, Madera County, (Herman and Jankiewicz, 1943).

N. filicollis.—Odocoileus hemionus. Hopland Field Station, Mendocino County, (Longhurst and Douglas, 1953).

N. spathiger.—Odocoileus hemionus. Hopland Field Station, Mendocino County, (Longhurst and Douglas, 1953).

Crenosoma mephitidis.—Mephitis mephitis. San Francisco and Marin County, (Hobmaier, 1941); *Spilogale gracilis.* San Francisco, and Marin County, (Hobmaier, 1941).

C. goblei.—Procyon lotor. Calaveras Dam, Alameda County, (Dougherty, 1945).

Parelaphostrongylus odocoilei.—Odocoileus hemionus. California Coast Range, (Hobmaier and Hobmaier, 1934).

Heligmosomum sp.—*Peromyscus boylei.* Hastings Reservation, Monterey County.*

Heligmosomoides sp.—*Neotoma fuscipes.* Hastings Reservation, Monterey County, Linsdale and Tevis, 1951).

Nematospiroides dubius.—Mus musculus. California, (Dikmans, 1940).

Glyptostrongylus collaris.—Macrotus californicus. Riverside County, (Neyland, 1955).

Molinostrongylus delicatus.—Tadarida mexicana. Berkeley, Alameda County.*

Allintoshius sp.—*Antrozous pallidus.* Arroyo Mocho, 6.5 mi. S.E. Livermore, Alameda County.*

METASTRONGYLIDAE

Dictyocaulus filaria.—Odocoileus hemionus. Hopland Field Station, Mendocino County, (Longhurst and Douglas, 1953).

D. viviparus.—Odocoileus hemionus. Hopland Field Station, Mendocino County. (Longhurst and Douglas, 1953), and Hastings Reservation, Monterey County, (Linsdale and Tomich, 1953).

D. hadweni (= *D. viviparus* ?).—*Odocoileus hemionus.* California, (van Roekel, 1929).

Angiocaulus gubernaculatus.—Mephitis mephitis. Pine Valley near Hastings Reservation, Monterey County, (Dougherty, 1946); *Taxidea taxus.* Pine Valley near Hastings Reservation, Monterey County, (Dougherty, 1946).

Parafilaroides decorus.—Zalophus californianus. California Coast, (Dougherty and Herman, 1947).

P. nanus.—Eumetopias jubata. California Coast, (Dougherty and Herman, 1947).

P. prolificus.—Eumetopias jubata. California Coast, (Dougherty and Herman, 1947).

P. sp.—*Eumetopias jubata.* California Coast, (Dougherty and Herman, 1947).

Pharurus convolutus.—Phocoena phocoena. San Francisco Bay, (Dougherty, 1943).

Stenurus vagans.—Phocoena phocoena. San Francisco Bay, (Dougherty, 1943).

Halocercus invaginatus.—Phocoena phocoena. San Francisco Bay, (Dougherty, 1943).

H. kirbyi.—Phocoenoides dalli. San Francisco Bay, (Dougherty, 1944).

FILARIIDAE

Setaria cervi.—Odocoileus hemionus. Hopland Field Station, Mendocino County, (Longhurst and Douglas, 1953).

S. labiato-papillosa.—Odocoileus hemionus. California, (van Roekel, 1929).

DIPETALONEMATIDAE

Wehrdikmansia cervipedis.—Odocoileus hemionus. Hastings Reservation, Monterey County, (Linsdale and Tomich, 1953), Lake County,* Truckee, Nevada County, (Annereaux, 1941), thirteen Counties in California (Herman and Bischoff, 1946).

SPIRURIDAE

Mastophorus dipodomis.—Dipodomys merriami. San Bernardino County, (Read and Millemann, 1953); *D. panamintinus.* San Bernardino County, (Read and Millemann, 1953); *D. deserti.* California;* *Perognathus* sp. Joshua Tree National Monument.*

Gongylonema neoplasticum.—Dipodomys merriami. Victorville, San Bernardino County, (Read and Millemann, 1953); *D. panamintinus.* Victorville, San Bernardino County, (Read and Millemann, 1953).

THELAZIIDAE

Thelazia californiensis.—Canis latrans. Big Bear Lake, San Bernardino County, and San Simeon, San Luis Obispo County, (Herman, 1949); *Ursus americanus.* California, (Hosford, Stewart and Sugarman, 1942); *Odocoileus hemionus.* Sequoia National Park, (Oberhansley, 1940); Cloverdale, Sonoma County (Herman, 1944), Hopland Field Station, Mendocino County, (Longhurst and Douglas, 1953), and Hastings Reservation, Monterey County, (Linsdale and Tomich, 1953).

Metathelazia californica.—Lynx rufus. Lassen County, (Skinker, 1931).

PHYSALOPTERIDAE

Physaloptera turgida.—Didelphis virginiana. Los Angeles.*

P. maxillaris.—Rattus norvegicus. Alameda, Alameda County;* *Mephitis mephitis.* California, (Morgan, 1941).

P. torquata.—Taxidea taxus. California, (Morgan, 1941).

P. rara.—Urocyon cinereoargenteus. California, (Morgan, 1941).

P. sp.—*Citellus nelsoni.* Panoche Pass, San Benito County.*

RICTULARIIDAE

Rictularia dipodomis.—Dipodomys merriami. San Bernardino County, (Read and Millemann, 1953); *D. panamintinus.* San Bernardino and Inyo Counties, (Read and Milleman, 1953); *D. morroensis.* San Luis Obispo County, (Read and Milleman, 1953).

TRICHURIDAE

Trichuris citelli.—Citellus beecheyi. Hastings Reservation, Monterey County, (Chandler, 1945), and Calaveras Dam, Alameda County.*

T. perognathi.—Perognathus californicus. Hastings Reservation, Monterey County, (Chandler, 1945).

T. fossor.—Thomomys bottae. Hastings Reservation, Monterey County, (Chandler, 1945), and Calaveras Dam, Alameda County.*

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TRICHINELLIDAE

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Hyalostelia Ancora Gutschick in the Mississippian of Indiana and Kentucky

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Abstract

Spicules of the sponge, *Hyalostelia ancora*, are reported for the first time from the Brodhead formation (middle Osagian) of Kentucky and the New Providence formation (lower Osagian) of Indiana and Kentucky; thus, the geologic range of the genus is extended down to the lower Osagian. Two more occurrences of the spicules in the Floyds Knob formation (upper Osagian) in Indiana and Kentucky are noted. *Hyalostelia ancora* is widely distributed throughout the Osagian rocks of southern Indiana and northern Kentucky.

Fossils associated with *Hyalostelia ancora* as well as the lithologies of the enclosing rocks are noted. *Hyalostelia ancora* was capable of living in a wide range of environments, but seemingly preferred environments favorable to the growth of crinoidal biotherms and/or deposition of limy muds (and these muds with well developed megafossil faunas).

Hyalostelia is considered to be restricted to the Mississippian and Pennsylvanian, and may have regional and local stratigraphic value.

In 1954 Gutschick described a new species of sponge, *Hyalostelia ancora*, from spicules found in the upper Osagian Floyds Knob formation of Indiana and Muldraugh formation of Kentucky. This was the first species of the genus to be reported from the Mississippian of North America.

Hyalostelia ancora is here reported for the first time from the Brodhead formation of Bullitt County, Kentucky and from the middle and lower New Providence formation of Clark County, Indiana and Jefferson County, Kentucky; the geologic range of the genus is thereby extended downward to the lower Osagian.

In addition, the present paper records two more occurrences of *Hyalostelia ancora* from the Floyds Knob formation: one from the Floyd County, Indiana and the other from Jefferson County, Kentucky.

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Methods

The plastic shales of the New Providence formation and the shaly siltstones of the Brodhead formation were washed with sodium bicarbonate. Limestones of the Floyds Knob formation were dissolved in dilute or concentrated hydrochloric acid.

List of Localities

Spicules of *Hyalostelia ancora* were found at the following localities:

1. Kenwood Hill in the southern part of Louisville, Jefferson County, Kentucky. Specimens found in the lower and middle New Providence formation 23 to 27 feet, 28

to 30 feet, 105 feet, and 117 to 122 feet above the top of the Kinderhookian shales.

2. East quarry of the Coral Ridge Brick Company at Coral Ridge, Jefferson County, Kentucky. Specimens found in the lower and middle New Providence formation 20 feet, 28 feet, and 72 to 78 feet above the calculated top of the Kinderhookian shales.

3. Outcrop on road 1.5 miles north of Carwood, Clark County, Indiana. Specimens found in the middle New Providence formation.

4. Outcrop on State Highway 44, immediately west of Knob Creek Church, Bullitt County, Kentucky. Specimens found in the Brodhead formation.

5. Mitchell Hill, Jefferson County, Kentucky. Specimens found throughout the 11 feet 10 inches of the Floyds Knob formation.

6. Spickert Knob, 3.5 miles northwest of New Albany, Floyd County, Indiana. Specimens found in the Floyds Knob formation.

DESCRIPTION OF THE SPECIES

The writer's spicules of *Hyalostelia ancora* fit so well Gutschick's description of the species that little further systematic information can be added. Anatetraene, hexactinellid, and oxyaster forms of the spicules were found and all except the last are figured. Only spicules from the New Providence formation are figured because they are the best preserved (figs. 1-9). The anatetraene form is rare; out of about 60 spicules, most of which were hexactinellid, only two anatetraene forms were noted. Measurements of the figured spicules are given in table 1.

ECOLOGY

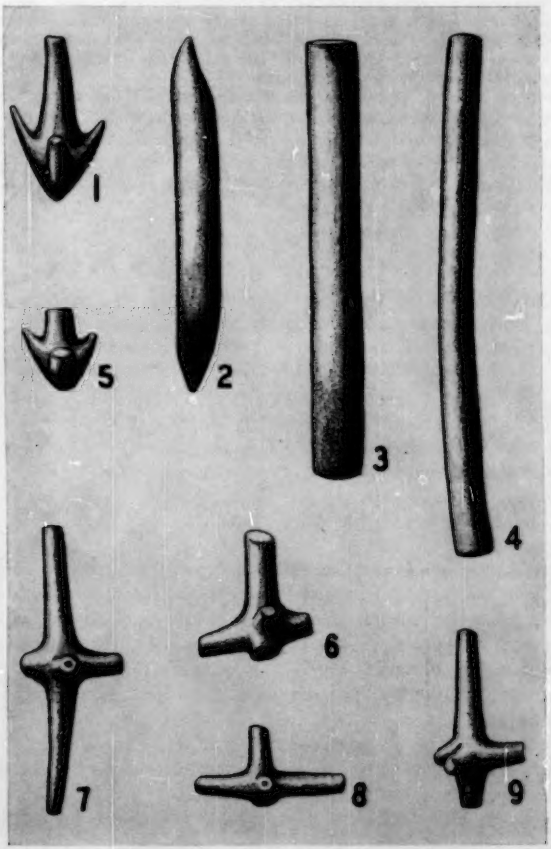
Hyalostelia ancora occurs in the Floyds Knob formation at Mitchell Hill (Locality 5) in oölitic and crinoidal limestones in association with bryozoans, brachiopods, echinoid spines, corals, worm tubes, and ostracods. The environment of deposition of these limestones has been interpreted as an offshore shallow sea (Conkin, 1954). A similar environment of deposition is suggested for the Floyds Knob crinoidal and oölitic limestones at Spickert Knob (Locality 6).

Hyalostelia ancora occurs in the shaly siltstones of the Brodhead formation at Knob Creek Church (Locality 4) in association with crinoids, corals, brachiopods, bryozoans, gastropods, and ostracods.

In the grey-green shales of the middle New Providence formation (Locali-

TABLE 1.—Measurements of figured spicules in millimeters.

Spicule	Greatest length	Diameter of shaft
1	0.92	0.20
2	2.08	0.25
3	2.67	0.30
4	3.00	0.20
5	0.56	0.17
6	0.69	0.17
7	1.62	0.15
8	0.83	0.13
9	0.99	0.13



Figs. 1-9.—*Hyalostelia ancora* from Indiana and Kentucky (all figures X 25). 1-4. Anatetraene forms from the lower New Providence formation on Kenwood Hill, southern Louisville, Jefferson County, Kentucky; 2. Spicule with worn extremities; 5. Anatetraene form from the middle New Providence formation 1.5 miles north of Carwood, Clark County, Indiana; 6, 8, 9. Hexactinellid forms from the middle New Providence formation 1.5 miles north of Carwood, Clark County, Indiana; 7. Hexactinellid form from the lower New Providence formation in the east quarry of the Coral Ridge Brick Company, Coral Ridge, Jefferson County, Kentucky.

Figured and unfigured spicules are deposited in the Dept. of Micropaleontology, American Museum of Natural History, Catalogue Nos. AS-3000 to AS-3012: AS-3000—fig. 1 (locality 1); AS-3001—fig. 2 (loc. 1); AS-3002—fig. 3 (loc. 1); AS-3003—fig. 4 (loc. 1); AS-3004—fig. 5 (loc. 3); AS-3005—fig. 6 (loc. 3); AS-3006—fig. 7 (loc. 2); AS-3007—fig. 8 (loc. 3); AS-3008—fig. 9 (loc. 3); AS-3009 (loc. 1); AS-3010 (loc. 2); AS-3011 (loc. 3); AS-3012 (loc. 4).

ties 1, 2, and 3) *Hyalostelia ancora* is associated with crinoids, bryozoans, brachiopods, corals, gastropods, pelecypods, trilobites, and ostracods.

In the plastic bluish-grey shales of the lower New Providence formation (Localities 1 and 2) *Hyalostelia ancora* is associated with a dominantly molluscan fauna; this association lends evidence for a near shore shallow sea environment.

Gutschick (1954) reported *Hyalostelia ancora* from crinoidal bioherms and crystalline limestones in the Floyds Knob and Muldraugh formations.

Further, throughout most of the New Providence formation and in parts of the Brodhead formation there are arenaceous foraminifers associated with *Hyalostelia ancora* (foraminifers have not been reported previously from these formations).

From a consideration of its occurrences in the stratigraphic section, it is clear that *Hyalostelia ancora* is widely distributed in the Osagian rocks of southern Indiana and northern Kentucky. Its association with several different types of rock and groups of fossils indicates that the sponge was capable of living in a wide range of sedimentary environments. *Hyalostelia ancora* seemingly preferred environments that were favorable to the growth of crinoidal bioherms and/or in which well-developed invertebrate assemblages grew and left remains in clayey, calcareous shales. However, it is certain that *Hyalostelia ancora* could tolerate much silt as witness its occurrence in the shaly siltstones of the Brodhead formation.

STRATIGRAPHIC VALUE OF HYALOSTELIA

At present the stratigraphic importance of *Hyalostelia* is uncertain because too few occurrences have been reported to determine fully the geologic range of the genus. However, until evidence is cited to the contrary, *Hyalostelia* may be considered to be restricted to the Mississippian and Pennsylvanian.

Locally and regionally, *Hyalostelia* may have stratigraphic value, but sponge spicules should be used in stratigraphy with caution as their genetic and specific relationships are often in doubt. Gutschick (1954) has noted that there may be more than one species of sponge represented by the spicules which are now referred to *Hyalostelia ancora*.

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Known Dispersal Rates and Migratory Potentials as Clues to the Origin of the North American Biota[1]

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Wolfson's (1955) interpretation of the origin of the North American avifauna from the standpoint of continental drift emphasizes some of the problems of biogeography, but contains two serious flaws that are bound to mislead the unwary. First, in making a case for continental drift as an explanation of contemporary faunal distribution, he ignores the great physical difficulty involved in explaining a sudden and geologically quite recent drift. Second, in view of contemporary observations, he quite needlessly manufactures difficulties attendant on the use of migration routes little different from those now existent.

It is beyond the scope of this paper to attempt a detailed explanation of the North American biota. We must first briefly consider the physical aspect of continental drift. We shall next take up examples of known plant and animal dispersal rates, sea passages by land birds, and the efficacy of water barriers. To test the indicated effectiveness of the northern dispersal routes we shall then briefly compare the biota of Central and South America with that of comparable latitudes in Africa and Australasia.

Acknowledgments.—I am indebted to Mr. W. Earl Godfrey for many suggestions concerning the ornithological aspects of this paper and for reading the preliminary manuscript. Many of the botanical aspects were discussed with Dr. W. G. Dore and Dr. C. Frankton, whose assistance is also gratefully acknowledged. Mr. George L. Robertson, Department of Transport, has supplied climatic and meteorological data in connection with problems of bird movement.

The Physical Difficulty of a Delayed Continental Drift

To realize how improbable is the occurrence of a pronounced continental drift late in geological time, we must consider the early part of the earth's history. The large mass of the moon (1/81 of that of the earth) and its high density (3.6) preclude the possibility that it was formed by gaseous condensation when the earth and the remaining planets were formed. It is generally conceded that it must have been formed by disruption from the already fluid earth, when the parent body has a period of rotation of about 4 hrs., through a resonant vibration set up by the solar tide. The size and depth of the Pacific Ocean basin, in comparison with those of the other oceans, and the instability of the Pacific rim have led to the logical supposition that the Pacific basin represents the scar of the moon's birth. If we accept

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this view we are forced to agree that at the time of the moon's abstriction the earth's crust was just starting to solidify. If the earth had been completely fluid, no scar would have been left; if solidification had proceeded far, the period of vibration would have been much less than the 2-hr. period of the solar tide and the moon would not have been formed.

Although no wholly acceptable explanation of the restabilization of the earth's crust after the formation of the moon has yet been put forward, it seems clear from the behavior of molten or plastic metals and other semisolid materials that rapid compensatory movements of the crust must have started as soon as the moon was torn away. These movements must have proceeded with diminishing speed until approximate equilibrium was achieved. It seems inconceivable that the continental masses, which must have been shattered by vibration when the moon was formed, lay huddled on one side of the earth for 2,000,000,000 years, during which solidification of the crust became complete, and then sped apart with great rapidity. (It will be recalled that Köppen and Wegener (1924), on whose version of continental drift Wolfson's interpretation is based, postulated a movement starting in about Cretaceous time and proceeding through the Pliocene.) I do not deny that some coastal patterns, in particular the opposed coasts of Africa and South America, support a pattern of breakup somewhat as postulated by Köppen and Wegener; but it seems to be physically impossible for it to have occurred after the origin of life. Accordingly it must be understood that the terms drift and permanence are used in this paper only in reference to continental movements recent enough to have any bearing on contemporary faunal and floral distribution patterns.

It has been evident that the powerful new tool available in paleomagnetism should eventually throw light upon continental drift as well as polar wandering, which is also of great concern to the biogeographer. After this paper was nearly completed Runcorn (1955) opportunely published his preliminary account of paleomagnetic studies in Arizona. He demonstrates the substantial agreement of determinations of positions of the north pole, from pre-Cambrian times onward, from paleomagnetic samples taken in Europe and Arizona. As Runcorn states, "the results appear to dispose of the possibility that since pre-Cambrian times the continents of America have drifted any appreciable distance from the continents of Europe and Africa".

CONTEMPORARY ARCTIC BIRD MIGRATION PATTERNS

It will be recollected that Mayr (1946) treated the North American avifauna as being of seven elements: Unanalyzed, Pantropical, Panboreal, Old World, North American, Pan-American and South American. Only the first four of these categories bear upon the present problem. Of these four elements, the Unanalyzed, Panboreal and Old World are (except for several families of oceanic and shore birds that are noted for making long sea passages) made up of families that are predominantly boreal or have many boreal representatives. The Pantropical element is a small one, consisting of three families of land birds and five that are aquatic or marine; the latter presumably capable of making sea passages with comparative ease. Thus the great majority of the land birds that occur in both North America and the

Old World are conspicuously boreal. This fact itself markedly suggests that most intercontinental dispersal has been by northern routes and minimizes the necessity for invoking continental drift. It is similarly significant that the farther north we go in North America the more closely does the flora in the northeast resemble that of Europe and in the northwest that of Japan and eastern Siberia; and that within the arctic a large proportion of the plants are specifically or subspecifically identical with those of Eurasia. We shall accordingly examine some examples of range changes dating from Pleistocene or post-Pleistocene times, and of oceanic jumps and other marked invasions that have occurred in historic times, to illustrate the ability of many organisms to utilize existing migration routes.

Wolfson assumes that the theory of permanence makes the Bering Strait the only biotic connection between North America and Eurasia. Although the Bering Strait must have been the only important migration route for land mammals other than arctic species, this assumption is palpably false for birds and for land plants.

Wolfson may be pardoned for overlooking the botanical links between northwestern Europe and northeastern Canada via Iceland and Greenland; but he should have recalled that several Old World birds regularly pass in spring northward through western Europe and westward by Iceland and Greenland into Canada. Because this is the more difficult and the less emphasized of the northern routes I shall stress examples that apply to it. Some species, like the Arctic Tern (*Sterna paradisaea*), the Ringed Plover (*Charadrius h. hiaticula*), the Old World Knot (*Calidris c. canutus*) and the European Ruddy Turnstone (*Arenaria i. interpres*) are powerful fliers and might be thought to constitute a special case; but the Fieldfare (*Turdus pilaris*) and the Greenland Wheatear (*Oenanthe o. leucorhoa*) are unexceptional fliers with the typical passerine wing form adapted to maneuverability and efficient flight at low speeds rather than to high speed and endurance. If these latter species can regularly make such sea passages almost any bird might. Various other European species or subspecies are known to make this crossing occasionally. One wonders whether some other northern birds whose European and Canadian populations are indistinguishable, such as the Lapland Longspur (*Calcarius l. lapponicus*) and Snow Bunting (*Plectrophenax n. nivalis*), do not also often make the crossing. All these birds have set up this trans-Atlantic migration route in a few thousand years since the Pleistocene; and it is reasonable to suppose that some will eventually send streams of autumn migrants southward through Canada and the United States, initiating wholly American populations.

NEARCTIC PLANT DISPERSAL RATES

Many plant distribution patterns provide inconclusive evidence of dispersal rates because the area of distribution may include more than one possible glacial refuge, but a few unambiguous examples will be given. It must be noted that although Hultén (1937) followed Fernald (1925) in assuming glacial refuges in which plants persisted through the Wisconsin glaciation in e.g. Gaspé Peninsula, Newfoundland, Northern Labrador and western Green-

land, Flint (1947) and Flint *et al.* (1949) have shown beyond reasonable doubt that these areas were completely glaciated; and the famous nunatak theory has fallen into disrepute among most botanists familiar with the areas involved. It may thus be assumed that the last glaciation was complete in all eastern Canada, all northern Canada with the possible, but improbable, exception of a little of the northernmost part of the arctic archipelago, and all but the extreme northern tip of Greenland. In contrast there was a large unglaciated area in Alaska, which just extended into the Yukon; and several parts of Iceland were free of ice.

Alchemilla glomerulans, a predominantly European plant, occurs in northernmost Quebec and Labrador. It may have survived the last glacial age in Iceland, where it presently occurs; but it must have spread at least from there to its present limits since the ice retreated from the coast of Greenland. Incidentally its rust, *Trachyspora intrusa,* has made the same journey. *Gentiana nivalis* also occurs in Scandinavia, Iceland, Greenland and northern Labrador; it must have spread at least from Iceland to Labrador since the Pleistocene.

Dryas integrifolia and *Saxifraga tricuspidata* were both almost certainly confined to Alaska in the last glaciation. (The latter species seems only to have segregated from *S. bronchialis* during the last interglacial age.) Both these plants have reached east Greenland. *Dryas* has plumed achenes, which facilitate dispersal by wind; but *Saxifraga* has no adaptations for long-range spread, yet *S. tricuspidata* has in a few thousand years spread eastward approximately 2500 miles and across several water barriers. Admittedly a considerable proportion of its route has been over ice or across land with low relief, yet this plant has also spread at least 700 miles southeastward into eastern British Columbia across country with extremely high relief.

Regardless of their pre-Wisconsin distributions all the plants that now occur in Greenland, with the possible exception of a few high arctic species, must have made at least one sea passage of some 200 miles or more in post-Pleistocene times. Whether they were carried by pack ice, blew across solid ice, were accidentally carried by birds or mammals, or were transferred in the mud layer of iced komatik runners is immaterial. They all made such a passage by essentially natural means.

If we included plants that seem to have made the northern North Atlantic crossing in interglacial rather than postglacial times we could include an impressive total; for many species that are absent from eastern Asia and/or western North America show continuous patterns of distribution across the North Atlantic land areas. For example, *Epilobium hornemannii* is absent from the Urals to eastern Siberia, but occurs across North America and in Greenland, Iceland and Scandinavia. *Carex norvina* has essentially the same distribution. These are both quite modern plants and this pattern probably dates from one of the interglacial periods. *Saxifraga aizoon* constitutes an even more convincing example. Both its morphology and its parasite relationships (Savile, 1954), indicate that this is one of the more modern species of a quite modern genus. It cannot have arisen much before the close of the Tertiary. In its several varieties it occurs in western Eurasia and northeastern

North America. It is moderately common in the Canadian eastern arctic, and extends south to Maine and Vermont, and west to Saskatchewan. It may have reached North America before the Wisconsin glaciation and survived it in mountainous parts of the eastern United States. It is a moderately calciphilous arctic-alpine plant, which, if it had ever been in western North America, could hardly have failed to persist in the Cordillera. The fact that its rust, *Puccinia pazschkei* var. *pazschkei*, has not yet reached North America, although it is fully as mobile as other saxifrage rusts that have covered the ranges of their host plants, is further evidence that *S. aizoon* reached North America quite recently. Its pattern of distribution makes it virtually certain that its access to North America was by the Iceland-Greenland route.

The preceding examples have been selected to illustrate particular patterns in connection with the northern Atlantic route. They are not necessarily particularly fast-moving species. It must be remembered that most of the plants that now grow in central Canada must have travelled more than 1000 miles since Wisconsin time. Even in the highly dissected Cordillera the rate of spread has been nearly as high for some plants. For example, *Hemieva ranunculifolia* and *Montia linearis* have spread northward in British Columbia some 600-700 miles beyond the edge of the Cordilleran ice sheet. As these are lowland rather than alpine plants they may well have come from substantially farther south. It may be noted that neither of these plants possesses burs, plumed seeds or any other device for long-range dispersal. Some Cordilleran plants may have spread substantially faster, but no estimate is possible for those that may have occupied more than one glacial refuge.

The distribution patterns of plants in the neighborhood of the Bering Strait, of which Hultén (1937) gives numerous examples, clearly show that many species traversed this area, mainly at least while the sea level was depressed in the last glaciation, and have traveled hundreds of miles east and west from the strait since the ice retreated.

Thus it seems that 100 to 200 miles per 1000 years is a common rate of spread for many plants under favorable conditions. In any of the three interglacial ages of the Quaternary period, estimated by Flint (1947) to have ranged from about 125,000 to 275,000 years, plants with such a potential rate of spread might easily disperse throughout the world. During the glacial periods, each of about 100,000 years, many temperate plants may have crossed the equator.

When we see these circumpolar distribution patterns developing before our eyes it is curious to recollect that Croizat (1952) ridicules the very possibility of "holarcticism." We are not, of course, here concerned with the area of origin of the flowering plants (if indeed so vast a group in its gradual development over a long period can be said to have originated in a single area), but it is necessary to refute Croizat's implication that the holarctic region could have played no part in their development or distribution.

TEMPERATE PLANT DISPERSAL RATES

It may justifiably be argued that the migration rates given for plants reoccupying deglaciated country cannot be applied to plants that must pass through densely vegetated country; although, indeed, many such plants are

not pioneers and only invade deglaciated country after it has become adequately vegetated. For information on penetration of fully vegetated country we must depend largely on data from plants introduced into new regions in historic time. Unfortunately the majority of such introductions are weeds of arable or waste land, which are subject to transportation along roads and railroads; or are cultivated plants that may escape into natural habitats from any point in their range of cultivation. Such plants seldom yield any useful data. However, *Epipactis helleborine*, a woodland orchid, has reached the midwestern United States and is spreading fast in the east. A few terrestrial plants may be mentioned that occur principally in native grassland. *Carex leporina*, *C. flacca* and *Luzula luzuloides* of Europe are widespread in the eastern United States, the first having reached the summit of Roan Mt., Tenn. (6300 ft.), and the last having spread as far west as Minnesota. Various plants of wet ground, which are not seriously subject to artificial dispersal, have spread conspicuously. Thus *Cardamine pratensis*, *Lathyrus pratensis*, *L. tuberosus*, *Lythrum salicaria*, *Centaurium umbellatum*, *C. pulchellum*, *Myosotis scorpioides* and *Veronica beccabunga* have all spread from the Atlantic coast to the Great Lakes or beyond, some 300 to 1000 miles, in 350 years or less. Some aquatic plants have spread hundreds of miles, much of the distance upstream, in equally brief or briefer periods. Notable examples are *Elodea canadensis* in the rivers of western Europe, *Butomus umbellatus* in the St. Lawrence and its tributaries, and *Eichornia crassipes* in the southern United States.

In view of these observed rates of dispersal and those indicated in the preceding section, Good's (1953) claim that the available means of dispersal fail to account for observed distribution must be regarded as unfounded.

RATE OF SPREAD OF INTRODUCED SPECIES

Limited introduced populations that have succeeded in crossing a substantial barrier sometimes remain approximately static or are crowded out by competing native species; but such invaders are often spectacularly successful. Many introduced plants are by nature invaders of disturbed areas and consequently tend to be aggressive agricultural weeds. We should remember, however, that organisms unaggressive in their original territory may become aggressive and pervasive when they invade new territory. Introduced birds and mammals often illustrate this point. The House Sparrow (*Passer domesticus*) and Common Starling (*Sturnus vulgaris*) in North America illustrate the tremendous speed with which introduced birds may spread. They were admittedly somewhat aggressive species even in Europe, but some of the much less aggressive English birds spread very rapidly when introduced into New Zealand. The Grey Squirrel (*Sciurus carolinensis*) spread rapidly when introduced into England and soon became a thorough pest. The recent northward spread of the Armadillo (*Dasypus novemcinctus*) in the southern United States illustrates how an animal may occasionally suddenly increase its range without crossing any substantial barrier.

It is still too soon to assess the status of the Cattle Egret (*Bubulcus ibis*) in America, but its early progress suggests that it may spread far and perhaps compete with some of the native herons.

There can be little doubt that some of the plants and animals that crossed the Bering Strait soon afterward not only achieved wide geographic dispersal, but also underwent great evolutionary diversification, perhaps through some mechanism similar to that proposed by Mayr (1954). For example, an early saxifragaceous plant, probably the immediate ancestor of *Mitella* and *Tiarella*, crossed from eastern Siberia into northwestern North America and gave rise to a remarkable assemblage of Cordilleran genera, a few of which have since spread back into eastern Asia.

METHODS OF RAPID DISPERSAL OF BOREAL PLANTS

Although we cannot undertake to discuss the vast field of methods of plant dispersal, to which Ridley (1930) devoted a large book without exhausting the subject, it seems advisable to say something of two methods that are particularly applicable in northern regions, both of which have been inadequately appreciated.

The first of these methods is wind action in the arctic. Polunin (1955) has recently discussed some phases of this topic. It may be difficult for any botanist who has not worked in the arctic either in winter or before the snow has begun to soften in spring to appreciate the efficiency of this mechanism in distributing plants of exposed habitats. Much of the Canadian arctic has low relief, with the ridges of rock smoothly planed into shallow curves by glacial action. Snow all but fills the intervening gulleys and crevices, so that the winter terrain varies from dead level to gently undulating. Gale force winds are so frequent that the wind-packed snow forms a smooth surface so hard that one can scarcely mark it with a boot heel. Rock crests and beach ridges, with smoothly convex surfaces, function as venturis, the wind speeding up as it passes over them and keeping them almost perpetually bare of snow. Plants of these exposed, arid situations, such as *Saxifraga tricuspidata* already mentioned, not only have their seeds or fruits readily transported; but, if broken loose by the wind or other means, are whipped bodily away, to disappear in a matter of moments. There is no question but that such plants, often with seeds in their capsules if the previous season was short, are sometimes blown hundreds of miles in a single gale. Many such plants must lodge in unfavorable sites or be lost in open leads in the sea ice, but a small proportion must make successful long passages. It is no wonder that some of these plants have traveled so far since the Pleistocene or that they show circumpolar homogeneity.

The second of these dispersal methods is the carriage of seeds by birds, particularly of various aquatic plants by waterfowl. Many aquatic plants, notably *Potamogeton* spp., occur sporadically over wide areas, being plentiful in one lake or group of lakes but absent from others within a few miles. Their distribution shows no clear pattern explainable by river systems or topography. Although they are so unexpectedly absent from some bodies of water, a number of these plants have circumboreal or occasionally nearly worldwide distribution. Of 37 species of *Potamogeton* listed by Fernald (1950) for the northeastern United States and southeastern Canada, 13 also occur in Eurasia. *Sparganium* spp., *Ruppia maritima, Zanichellia palustris, Triglochin*

maritima, *T. palustris*, *Alisma gramineum*, *Nymphaea tetragona*, and *Lemna* and *Spirodela* spp. are other North American aquatics that occur in Eurasia, a few also being known from South America and North Africa. *Lemna* and *Spirodela* are probably spread largely by adhering to the body feathers and feet of waterfowl as they rise from ponds in which these plants are growing. Seeds of many aquatic plants, notably *Potamogeton* spp., are eaten, along with other parts of the plants, by waterfowl, particularly the pond ducks (Anatinae). Guppy, quoted by Ridley (1930), showed that seeds of *Potamogeton*, *Sparganium* and various Cyperaceae taken from the intestinal tracts of wild ducks germinated freely; and he obtained 60% germination of seeds of *Potamogeton natans* taken from the droppings of domestic ducks, whereas uneaten seed showed only 1% germination. Although the uneaten seeds may have suffered from desiccation, there is a distinct suggestion that such seeds are definitely adapted to withstand passage through the intestinal tracts of birds. Guppy found the minimum time for passage through the tracts of domestic ducks to be about 7 hours, but concluded that, since many of the hard seeds must lodge, like gravel, in the gizzard, the maximum period must be much more. The Mallard (*Anas platyrhynchos*) and Pintail (*A. acuta*), which normally fly at about 55-65 m.p.h. and are wide-ranging species, must occasionally transfer viable seeds many hundreds of miles. It must be noted that this dispersal mechanism is more likely to be successful than more haphazard means of long-distance dispersal, for a large proportion of the transported seeds can be expected to reach a suitable habitat.

Seeds of many land plants must occasionally be transported by birds that habitually fly long distances. Geese, in grazing upon herbage, incidentally swallow many seeds, some of which pass through the intestines. We ordinarily think of the seeds of fleshy fruits being transported by such birds as thrushes and waxwings, which scatter the seeds along hedge-rows. However, longer-ranging birds that are not ordinarily frugivorous also take fruit on occasion. Some of the plovers and curlews fatten up on blueberries, etc., before their long fall migration flights. The Parasitic Jaeger (*Stercorarius parasiticus*) has been recorded feeding upon fruits of *Vaccinium vitis-idaea* and *Empetrum nigrum* both in Sweden (Ridley, 1930) and in Canada (Savile, 1951).

WATER BARRIERS AND DISPERSAL OF LAND ANIMALS

The effectiveness of substantial stretches of open water in preventing movements of land animals is clearly shown by the high degree of endemism in the Australian fauna. The remarkable number of marsupials surviving in that continent is certainly due in large part to the fact that the placental carnivores have been unable to reach it.

It is probable that arctic mammals occasionally make stages of the northern North Atlantic passage, as well as the shorter Bering Strait passage, on pack ice. But for most mammals sea passages of more than a few miles are almost completely effective barriers. Their effectiveness is attested by the number of species absent from Vancouver Island and Newfoundland that occur on the adjacent mainland. The former case is particularly striking, for parts of the channel between Vancouver Island and the mainland are less than 2 miles

wide. Nevertheless it is probable that some land mammals occasionally successfully swim distances of 10-15 miles. I recollect cases of stags swimming the Bristol Channel, a minimum distance of 11 miles, from Somerset in southwestern England to south Wales when pressed by hounds. It is possible that substantial groups of animals will rarely make similar crossings to avoid predators or when driven by forest fires.

The recolonization of Krakatau (Stehn, Docters van Leeuwen and Dammerman, 1929) since the eruption of 1883 that buried the remnant of that island and the two adjoining islands under a great depth of hot pumice and ash, and beyond question rendered them sterile, is instructive. It must be remembered that many plants could not survive on arrival unless pioneer plants had already provided a suitable habitat, and that most land animals could not survive until an ample flora was established. The rate of recolonization must therefore be regarded as impressive. By 1929 more than 200 species of flowering plants were established, and many birds and invertebrates had been recorded. Eight species of reptiles had colonized the islands, arriving either on driftwood or by swimming the minimum distance of about 10 miles. The only mammals present were three bats and two rodents, one of the latter thought to have been introduced by man but the other clearly having come by natural means. Even one naturally introduced mammal in a period of under fifty years, the first part of which was impossible for its survival, is a notable achievement. Given adequate time we may expect appreciable numbers of mammals to invade such islands.

OCEAN PASSAGES BY LAND BIRDS

Elsewhere than in the far north the Atlantic may be regarded as insuperable to land mammals and almost so to land plants, but it is occasionally traversed by land birds. The North American population of the Pintail (*Anas acuta*) is now recognized to be identical with that of Europe; and banding records suggest that it flies the North Atlantic quite frequently. Cooch (1952) has recorded a banded Pintail shot in England nine days after release in Labrador. The occasional occurrence of several European species of ducks in North America and of American species in Europe suggests that many members of the Anatidae are potential transoceanic colonists. The Lapwing (*V. vanellus*) crossed the North Atlantic from Europe to Newfoundland in large numbers on an easterly gale in December 1927. More remarkable is the fact that small North American land birds occasionally turn up in Europe; recent examples being the Yellowthroat (*Geothlypis trichas*) (Whitaker, 1955) and Myrtle Warbler (*Dendroica coronata*) (Smith, 1955) in England.

Most of these accidental crossings fail to establish the invading species; but the recent establishment of the Cattle Egret (*Bubulcus ibis*) of Africa in northeastern South America, and its incursion thence into southeastern North America where it has already bred at least once, show that they cannot be disregarded. The details of this incursion are summarized by Drury, Morgan and Stackpole (1953) and Godfrey (1954). There seems to be no reason to doubt that the Cattle Egret crossed the South Atlantic, some 1700 miles

at its narrowest, by unaided flight. From their wing-form and general behavior the herons are judged to be competent although not exceptional fliers. Bradlee, Mowbray and Eaton (1931) list no less than nine species of herons as occasional or regular visitors to Bermuda, some 600 miles from the American mainland. As most of these are spring or fall migrants, rather than winter residents, many of them are probably on passage between the West Indies and such points as Nantucket or Cape Sable; if so they would be making flights of 700-900 miles. The astonishing recent occurrence of the Little Egret (*Egretta garzetta*) in Newfoundland (Godfrey, 1956), after a presumptive minimum flight of over 2000 miles from Europe or Morocco, shows the endurance of which a heron may be capable.

After seeing one successful crossing of the Atlantic by a breeding population we cannot ignore the potentiality of the process. One such crossing in a thousand years would mean a thousand since the start of the Pleistocene, far more than enough to account for the similarities between bird faunas east and west of the Atlantic.

POSSIBLE ORIGIN OF MIGRATORY FLIGHTS ACROSS SEA BARRIERS

A digression must be made of this point to consider how migratory flights across substantial bodies of water may be established. There is some evidence that many cases of birds straying far beyond their usual limits are due to the occurrence of wind shifts during migration flights at night or in fog. Birds are very sensitive to wind direction, as is indicated by their virtually universal habit of landing and taking off into the wind even in a gentle breeze. In flight, wind direction can only be judged by visual cues, *i.e.* by lateral drift or enhanced or decreased ground speed, which are estimated by the apparent movement of the ground beneath the flying bird. If birds start a migration flight before dark they will set off with a clear impression of wind speed and direction derived from visual cues. Even if they start after dark they will have a reasonably good impression from the sensation of the wind upon them while they were stationary. But they have no way of detecting changes in strength or direction of the wind after dark while they are in flight. A violent frontal passage with a great increase in wind would be detected because it would cause turbulence for a few hundred feet above the ground; and it is probable that some birds would discontinue their flight under such conditions. But at moderate wind speeds no change in velocity will be detected if the ground is invisible.

A head wind will simply slow the birds down and daylight will find them still in familiar territory. What is likely to cause trouble is a change to a cross or tail wind of moderate speed. Such a shift early in the night may cause a navigational error of a hundred miles or so by morning, which may bring a bird into unfamiliar territory or over water. A bird lost in this manner apparently tends to keep flying down wind. A few examples will illustrate this thesis. On 11 June 1950 a Myrtle Warbler (*Dendroica coronata*) appeared at Chesterfield Inlet on the northwest coast of Hudson Bay, about 200 miles beyond its normal limits, during a gentle southerly breeze that had started the previous night. It flew into a building and, on release

from a south door, swung round and continued north across snow-covered ground. In mid-December 1952 a great flight of Brünnich's Murres (*Uria l. lornvia*) occurred in southern Quebec and eastern Ontario. This flight followed a sustained but quite gentle easterly breeze of several days' duration. It is suspected that this breeze started at night while the birds were flying off shore in the Gulf of St. Lawrence, that daylight found them inland, and that thereafter they simply wandered down wind. On 8 June 1952, my wife and I were astonished to see eight Arctic Terns (*Sterna paradisaea*) at Ottawa, Ontario. (Northern field work in the three preceding summers had fortunately made me intimately familiar with the field aspect of the species). It will be recalled that the Arctic Tern, after crossing the Atlantic at high latitudes in spring, migrates southward into Hudson Bay and James Bay. During the night of 6 June a cold front crossed James Bay and the wind behind it averaged north *ca.* 15 m.p.h., to judge from the records from Moosonee and Kapuskasing. If these birds were headed for the islands in southern James Bay, this unexpected tail wind would have carried them well overland by morning. On the morning of 7 June there was a fresh northwest breeze at Ottawa and the birds probably reached there that day by flying downwind. Griffin (1944) noted the tendency of Herring Gulls (*Larus argentatus smithsonianus*), released in unfamiliar territory, to wander downwind.

With more biologists visiting the north, numerous examples of birds substantially beyond their usual limits in northern Canada have recently come to light; and it is becoming clear that this overshooting in spring migration is not particularly rare. The phenomenon is not, of course, confined to North America. Long ago Nansen (1897) recorded Snow Buntings (*Plectrophenax nivalis*) seen from the *Fram* far north of Severnaya Zemlya and Novaya Zemlya in successive springs.

The Scotland-Faeroes-Iceland-Greenland-Baffin Island migration route probably arose by a succession of such accidents. The latest available charts of normal pressure distribution, published by the U.S. Weather Bureau (1952), show that by May the Icelandic low has greatly weakened and is centered south of Greenland. This pressure distribution means that, *on the average* at this time of year, a bird will have a gentle following wind all the way from Scotland, *via* the Faeroes, Iceland and southern Greenland to Baffin and thence southward to James Bay or Newfoundland. This is the semicircle flown completely by the Arctic Tern and in part by various other migrants. Admittedly birds will sometimes find unfavorable winds along this route, but tail winds must occur often enough to help establish this migration pattern and to support it when established.[2] By September the Icelandic low has begun to strengthen and is centered in Davis Strait, causing prevailing westerly winds across the southern tip of Greenland and gentle southerly or variable winds in the vicinity of Iceland. Thus conditions for the eastward

[2] The Fieldfare migrates from Europe to Iceland, but it recently established a sedentary colony in southwest Greenland by a winter flight of much the type described here, as has been described by Finn Salomonsen (The immigration and breeding of the Fieldfare (*Turdus pilaris* L.) in Greenland. Proc. 10th International Ornithological Congress (Upsala, 1950), 515-526. 1951).

fall migration are reasonably good, although not as favorable as those for spring. The striking feature about the September pressure distribution is that it indicates a substantial westerly wind from Labrador to the British Isles, which helps to explain the British occurrences of the Yellowthroat and Myrtle Warbler mentioned above.

Pressure distribution in the Bering Strait region suggests light north or northeast winds in both spring and fall migration periods; not markedly favoring migratory flights across the strait in either direction, but certainly not seriously hindering them. The somewhat limited incursions of migrants through Alaska into Anadyr are perhaps due to the high relief of the Cordilleran region having so delayed recolonization of Alaska that there has not yet been enough time for many species to establish migration flights across the strait.

Returning to the North Atlantic route we find that, if we include the Faeroes, the longest sea passage is about 250 miles and the others are each roughly 200 miles. If we exclude the Faeroes, which are admittedly a small target, the longest sea passage, from the Hebrides to Iceland, is about 460 miles. This distance is about three-quarters of that from Cape Hatteras to Bermuda. Bermuda, a much smaller target than even the Faeroes, is visited either occasionally or regularly by a surprising number of land birds. Apart from hawks, owls, shorebirds, swifts and swallows, which can be discounted as being powerful fliers, and sea birds, waterfowl and the herons already mentioned, Bradlee, Mowbray and Eaton list 39 species of land birds as occasional, frequent or regular visitors to the islands in winter or on migration. Regular visitors include the Belted Kingfisher (*Megaceryle alcyon*), Eastern Kingbird (*T. tyrannus*), Black-and-White Warbler (*Mniotilta varia*), Northern Waterthrush (*Seiurus noveboracensis*) and Snow Bunting (*Plectrophenax nivalis*). Other visitors include doves, cuckoos, woodpeckers, thrushes, larks, pipits, vireos, wood warblers, icterids and fringillids. Even the Ruby-throated Hummingbird (*Archilochus colubris*) is an occasional visitor. Many of these birds are passage migrants, presumably traveling roughly north and south, rather than between the islands and Cape Hatteras, and must regularly make overwater flights of 700-900 miles.

The performances of these Bermuda visitors make it clear that only perpetually foul weather could prevent the use of the Iceland-Greenland route by any bird with normal flying ability. They also suggest that much longer flights by groups of birds large enough to establish breeding populations are a practical possibility.

CENTRAL AND SOUTH AMERICAN BIOTA COMPARED WITH THAT OF COMPARABLE LATITUDES IN AUSTRALASIA AND AFRICA

To complete the picture we must briefly consider such similarities as occur between the flora and fauna of South America, Africa and Australasia, which have so largely influenced the proponents of continental drift. Actually the similarities, although occasionally striking, are so few in proportion to the whole biota, the dissimilarities so great, and the degree of endemism so high in all these areas, that the southern flora and fauna seem to offer the strongest

possible evidence in favor of permanence. If all the southern land masses had been grouped together for as long as the supporters of drift suppose, their biota should have been much more uniform.

In order to explain such similarities as we do find on the basis of permanence we have to assume: (a) passage across the Bering Strait, and from high northern latitudes across the equator and often to high southern latitudes; or (b) passage across the southern oceans.

That the Bering Strait has been crossed repeatedly by plants and animals in Pleistocene and post-Pleistocene times, although a land bridge was only intermittently available, is beyond question. The numerous plants that occupy what Hultén (1937) terms Beringia and Austroberingia clearly indicate the importance of this passage. In tertiary times Beringia was probably above sea level for much longer periods, and passage of plants and animals between Asia and America must have been relatively unrestricted.

Various plants have passed from high northern to high southern latitudes through the Cordilleran region. Some of these distributions are mapped by Hutchinson (1926). Thus the genus *Ribes* is circumboreal and runs south through the Cordillera to the extreme south of South America. *Empetrum* is also circumboreal but occurs elsewhere only in southernmost South America and the Falkland Islands. This genus apparently travelled along the Rockies and Andes but has disappeared from most of the route. These are moderately old genera and may have achieved this distribution very gradually over a long period, but some much more modern plants show similar patterns. *Carex* is a modern genus of the relatively advanced family Cyperaceae. Two species, or superspecies, shown by their morphology and parasite relationships to be fairly advanced members of the genus (Savile and Calder, 1953), are *Carex macloviana* and *C. magellanica*. Some segregates of the former have been made on slender although possibly valid grounds, and the North American population of the latter has been distinguished under the name *C. paupercula* without convincing evidence; but the world population of each is almost homogeneous. When we consider that each belongs to a plastic, rapidly evolving group it is hard to believe that the populations have been disjunct for much longer than the duration of the Pleistocene. We find that *C. macloviana* occurs in northwestern North America, from Gaspé Peninsula to Greenland, and in Europe; and that *C. magellanica* ranges widely across boreal North America and Eurasia. Both species occur elsewhere only in the southern tip of South America, both on the mainland and on the Falkland Islands. No variation of any continental drift hypothesis has placed the southern tip of South America close to any boreal region at any geological period. In view of the modernity of these plants and the minor distinctions of their disjunct populations, it is reasonable to suppose that they traversed the length of the Cordillera during a glacial period, when, for most of the distance, they presumably experienced a cool, pluvial climate, and that they have since become extinct in the tropical and warm temperate parts of their route. In view of known post-Pleistocene migration rates for many *Carex* spp. in Canada, any one of the glacial-interglacial cycles of the Pleistocene would have been ample for such a migration if no serious climatic or physiographic barriers were encountered.

Of the various groups of organisms that originated in and radiated from Asia or North America it was almost inevitable that a number should have reached the southern hemisphere in both the old and new worlds. It is also to be expected that a few should have failed to survive in their region of origin, owing to altered environment, competition or increased predation. Just as the Central American route to the southern hemisphere has intermittently been open, it is reasonable to believe that access to Africa and the Australo-Papuan region has sometimes been freer than at present. During pluvial periods amelioration of the desert areas of North Africa and Arabia must have greatly facilitated passage between Asia and Africa. Similarly, as pointed out by Mayr (1944), a lowering of sea levels by the amounts calculated for the Pleistocene glaciations, or a modest local raising of the continental shelf, would have been sufficient to connect all the western part of the Malay Archipelago, including Borneo and Bali, with continental Asia, and would have substantially increased the accessibility of Australia.

If a free connection through the Bering Strait region allowed a relatively homogeneous boreal population, then groups that dispersed southward from Asia and North America might be expected to develop quite similarly provided that they met environments that were not too dissimilar. However, if passage across the Bering Strait were greatly restricted, the Asian and North American populations would come to possess profound genetic differences and their southern radiants would not be likely to resemble each other closely.

The second alternative, direct passage across the southern oceans, although presumably rare, cannot be completely discounted insofar as land plants are concerned. Distribution patterns of genera or families linking South America with South Africa and/or Australia have been used in support of continental drift. Some such distribution patterns could be so explained; but there is another pattern that does not fit such an explanation at all, namely one that links eastern Australia, the eastern Malay Archipelago or New Zealand with western South America. Table 1, derived chiefly from Hutchinson (1926), gives some examples of this trans-Pacific pattern. The family Winteraceae is found additionally in some Pacific Islands. *Clethra* (Clethraceae) has a somewhat similar distribution to Winteraceae, but has also reached Madeira. The complete absence of these groups of plants from South Africa, western Australia and the Indian Ocean region, and their occurrence, sometimes in quite restricted latitudes, on both sides of the South Pacific are sharply at variance with any drift hypothesis that postulates contiguity of both coasts of the South Atlantic, and both coasts of the Indian Ocean, but complete separation of the coasts that now border the South Pacific.

If the possibility of a successful passage across the South Pacific seems remote, it must be remembered that one such successful accident in a million years throughout the Tertiary would more than account for all the disjunct distribution patterns of the type under discussion. We can only speculate as to the manner in which such ocean passages were made, but the carriage of seeds in crevices of floating logs is likely to have been important. In view of the heavy mechanical scarification or treatment with strong acids to which seeds of many plants must be subjected if prompt germination is to be secured, it is improbable that massive protective coats such as that of

TABLE 1.—Distribution of some South Pacific flowering plants

Genus and family	West Pacific distribution	East Pacific distribution
Eucryphia (Eucryphiaceae)	Tasmania, southeast Australia	South Chile
Jovellana (Scrophulariaceae)	New Zealand	Central Chile
Laurelia (Monimiaceae)	New Zealand	Central Chile
Lomatia (Proteaceae)	Eastern Australia	Western South America
Pernettya (Ericaceae)	Tasmania, New Zealand	Central America, western South America
Winteraceae	Southeast Asia, eastern Malay Archipelago, eastern Australia, New Zealand	South America generally

the coconut are generally essential to render seeds impervious to prolonged immersion in sea water. Cereal seeds, which lack impervious coats, withstand substantial periods of such immersion. The publicity that has attended recent raft voyages along the south equatorial current serves to emphasize that driftwood could cross from Peru to Australia or New Guinea in a relatively short time. The west wind drift in 40-50°S, although less interesting to the ethnologist than the equatorial current, is substantially stronger and would carry logs from Tasmania or New Zealand to Chile quite rapidly. Such passages would by no means be confined to strand plants, for any great river in times of flood carries trees to sea from far inland; and occasionally we see such trees borne by tide and wind far up into estuaries. The odds against such a successful carriage of seed once in a million years or so are certainly not prohibitive. It is at least preferable to invoke known ocean currents to account for distribution patterns of this sort rather than, like Croizat (1952), to propose for every disjunct pair a transoceanic land connection for which there is no geological support. Although transoceanic dispersal must be rare, it should be noted that when it does occur it is vastly more rapid than dispersal by most means across land.

The marked circumpolar uniformity of the arctic and boreal flowering plants and birds; and the increasing divergence as we move southward, culminating with the conspicuous differences between those of South America and Africa, lend support, as we have already seen, to the overwhelming importance of the two northern passages in providing biotic interchange. Because of the evidence that both land birds and land plants occasionally make successful ocean passages, it is desirable to use the distribution of land mammals, for which long sea passages are extremely improbable as a further check. If mammalian interchange between the old and new worlds has been almost confined to the Bering Strait bridge, the mammals of Central and South

America should be even more distinct from those of Africa and Australasia than are the land birds and land plants.

A tabulation was accordingly made of the distribution of the various families of mammals, excluding the Hominidae, Pinnipedia, Sirenia and Cetacea, all of which are capable of ocean passages. The figures are subject to minor modifications according to individual interpretations of family limits, but the general import is clear.

Out of 87 families surveyed, 48 are exclusively of the old world, 21 are exclusively of the new, and 18 currently occur in both hemispheres. These figures ignore recent introductions such as those of the Muridae into North America. Of the 18 common families 15 are either exclusively northern or have plentiful boreal or arctic representatives.

The remaining three families are chiefly tropical. One of these is a family of bats (*Emballonuridae*) of wide distribution, but with only one of ten genera common to the old and new worlds. It is reasonable to believe that these bats, like many land birds, might rarely make sea passages. The other families are Camelidae and Tapiridae. The camels appear from fossil evidence to have originated in North America, whence they diverged into South America and eastern Asia. Prior to domestication no camel seems to have reached western Africa, and no llamas occur in eastern South America; there is thus no evidence to support a trans-Atlantic link. The tapirs are currently restricted to South America except for one Malayan species. This disjunct distribution is explained by the widespread occurrence of the family in Tertiary times, notably in China and North America. The past and contemporary distribution is readily explained on the basis of passage through the Bering Strait bridge; but no form of continental drift hypothesis fits the distribution pattern, for the tapirs apparently never reached Africa.

Thirteen families of mammals are restricted to Central and South America, with at most minor incursions into southernmost North America. Eleven more families are restricted to Africa, or at most show minor incursions into Arabia. Thus the mammalian fauna of Central and South America is even more sharply distinct from those of the old world than are the avian fauna or the land flora. This is exactly what we should expect if the ocean barriers have always been effective and communication has always been predominately through the Bering Strait bridge.

The uniformity of the northern fauna, in contrast to those of more southern regions is reflected in the increasing tendency to recognize a holarctic region in place of separate palearctic and nearctic regions (Schmidt, 1954).

WOLFSON'S ARGUMENTS

Now, in the light of known performance, let us review some of the difficulties that Wolfson raises against continental permanence.

Speaking of Mayr's Unanalyzed element, Wolfson finds it most remarkable that in most of these families not only the family but lesser taxa, down frequently to subspecies, are widespread. Apart even from the oceanic groups, most of the families of this element include a high proportion of fast and powerful fliers; and a substantial number of the species today regularly make

long, often sustained migration flights, sometimes across many hundreds of miles of water. This element was divided by Mayr into four groups: oceanic birds, shore birds, freshwater birds (partly marine), and land birds. The first group presents no problem. The second consists almost exclusively of powerful fliers, of which many penetrate high arctic latitudes; some regularly cross the northern North Atlantic and the remainder unquestionably could do so. The third group is composed of nine families, representatives of all of which make substantial flights over water. The Colymbidae, Phalacrocoracidae and Anatidae currently have representatives that penetrate far enough north to make intercontinental passages by the two northern routes perfectly feasible. Representatives of the families Colymbidae, Phalacrocoracidae, Anatidae, and Rallidae visit Bermuda with some regularity; and species of Pelicanidae, Phoenicopteridae and Threskiornithidae are accidental visitors to the islands. The fourth group consists of Accipitridae, Pandionidae, Falconidae, Caprimulgidae, Apodidae, Picidae, and Hirundinidae. Of these seven families all but Picidae must be regarded as very powerful fliers; and all seven include regular visitors to Bermuda. Why, then, must it be regarded as remarkable that these families should be widespread under conditions of continental permanence?

Mayr's other elements are: Pantropical, Panboreal, Old World, North American, Pan-American and South American. The last three categories do not concern us. Of the other three the Old World element is the only one comparable in size with the Unanalyzed. Almost all the families of the Old World element have representatives that reach nearly to if not beyond treeline. Such species could easily make high latitude intercontinental passages by either existing northern route during xerothermic periods.

The Panboreal element consists of the families Gaviidae, Alcidae, Phalaropidae and some other shore birds. All these birds move freely across the northern seas and present no problem.

The Pantropical element is also a comparatively small one, of eight families. Five of these are fresh-water or partly marine families whose members are probably capable of long sea passages comparable with that recently achieved by the Cattle Egret. In fact it may justifiably be claimed that only the quite reliable navigational mechanism that most birds seem to possess has prevented such crossings from occurring with some frequency. The remaining families are land birds: Psittacidae, Trogonidae and Capitonidae. These are the only families that present any problem on the basis of continental permanence. In these families, one of which is very large, there is not a single genus common to the eastern and western hemispheres, which indicates that contacts must have been extremely scarce. In view of the large number of land birds that fly regularly 600 miles or more from North America to Bermuda, and the appreciable number that occasionally fly the full width of the North Atlantic, these figures supply small comfort to the advocate of continental drift.

In questioning whether all widely distributed organisms could have dispersed through the Bering Strait bridge, Wolfson points out that the strait probably never had a tropical or subtropical climate and that practically the whole region is subjected to arctic conditions of daylight. In view of

the importance of the photoperiod in controlling reproductive physiology of flowering plants and birds, he believes it unlikely that conditions of extreme day-length variation would have been conducive to free dispersal of subtropical and even temperate faunas and floras.

I agree that the Bering Strait region has probably never had a tropical climate and has always had pronounced day-length variation, but it must often have enjoyed a substantially warmer climate than at present. However, to assume that groups which we know today as tropical were thus debarred from Beringia is to deny all adaptability both in the species and in the evolutionary series. The hummingbirds are distinctly tropical, yet even today when we are scarcely out of a glacial age the Rufous Hummingbird (*Selasphorus rufus*) has extended its breeding range well into Alaska. How easily might such a species, in an interglacial period of 100,000 years or more, have established a breeding population in Anadyr and eventually have migrated down the China Coast.

It is surely reckless to assume that contemporary tropical animals spring from exclusively tropical ancestors when the fossil record repeatedly tells us otherwise. Contemporary elephants are tropical, but the mammoth (*Elephas primigenius*) survived in northern Siberia until about 15,000 years ago. Similarly a rhinoceros (*Dicerorhinus merkii*) occurred in central Europe as late as mid-Pleistocene (Zeuner, 1950). The lion (*Felis leo*), today a tropical species, ranged over much of Europe in the Pleistocene.

The photoperiod poses an interesting problem, but let us remember that there is no need to assume that conditions must have "been conducive to free dispersal" through the strait. The floral and faunal differences between adjacent parts of Asia and North America indicate that Beringia has been a selective filter. Presumably the organisms that made the passage *en route* between regions of lower latitude were generally those with adequate adaptability. We see on all sides examples of highly adaptable organisms, capable of mastering abrupt and extreme changes in environment. The Common Starling (*Sturnus vulgaris*) originated, in North America, from nonmigratory European stock; yet thirty years after it reached Ottawa, Ont., it was estimated that about 90% of the large local population had become regularly migratory. Even birds much less adaptable than the Starling may be expected to adapt themselves to severe climatic changes as fast as such changes occur. Why should not occasional representatives of predominantly tropical and nonmigratory groups of birds move gradually into areas such as Beringia during xerothermic periods and become migratory? With subsequent climatic deterioration the populations, possible with substantial genetic changes, would be pushed back to lower latitudes, but not necessarily to their ancestral ranges.

Many plants show marked ability to withstand conspicuous changes in daylength. Numerous high arctic species flower freely in middle latitudes, although restricted to high elevations where the temperature is low and competition not severe. I recall many temperate flowers, fruits, vegetables and cereals being grown successfully in the Kenya highlands within half a mile of the equator.

One of Wolfson's arguments against the general use of the Bering Strait is that as far as birds are concerned it seems to have been essentially a one-

way bridge. Although this may be largely true for birds, it is not so for flowering plants which have moved abundantly through it in both directions. The recent penetration into Anadyr of the Myrtle Warbler (*Dendroica coronata*) and Northern Waterthrush (*Seirus noveboracensis*) shows us that the westward passage is currently feasible for small birds of tropical affinities. If, during some geological periods, the westward crossing was more difficult it may well have been due to prevailing westerly winds in spring or some topographic peculiarity now hidden from us.

CONCLUSIONS

In view of the physical improbability of a substantial continental drift being delayed until the Cretaceous or later, dispersal rates and the migratory capacity of contemporary organisms across water have been examined. The capacity of many plants and animals in these respects is seen to be ample to account for a large proportion of disjunct distribution patterns. It is felt that these capacities and the capacity of both the species and the evolutionary series to adapt to environmental changes have been greatly underrated by proponents of drift. The overland rates of spread of many plants and animals and their adaptability to climatic variation; the observed movements of land plants and animals across ice and small water barriers; the substantial oceanic flights regularly made by many land birds; and the great degree of uniformity in the holarctic biota, with progressively increasing dissimilarity as one passes southward, combine to support a belief that the North American biota is most satisfactorily explained by the assumption that the continents have been essentially permanent in relative position and general outline, but that the Bering Strait and some other shallow sea barriers have intermittently provided land connections between the land masses adjoining them.

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A Taxonomic and Ecologic Study of the Flora of Monument Peak, Oregon[1]

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Monument Peak is located in Linn County, Oregon on the West flank of Cascades about 25 miles due west of Mt. Jefferson and the Cascade Divide, and approximately ten miles east southeast of Mill City, (Lat. N 44°42′ and Long. 122°20′ W). The region most of which lies within the Willamette National Forest is drained by the North Santiam River.

The taxonomic aims in this study were 1) to collect and identify all the species of vascular plants on the peak above 3700 feet and 2) to determine the affinities of the flora with those of other regions; while the ecologic objective was to recognize, delimit, and analyze the plant communities occurring in the region. A broad over-all objective was to gather data that might contribute to our understanding of the origins and relationships of the flora of Western Oregon. Alone it cannot aid materially in the realization of this broad objective, but it is believed that studies of such relatively undisturbed floras of isolated peaks west of the main range of the Cascades may when correlated yield significant information on the history of the region as a whole, and indicate trends of migration and the effectiveness of barriers to dispersal.

Two seasons, 1947 and 1948, were spent in the area collecting, observing, identifying and making statistical analyses. Determinations of species were made from fresh material in most instances. However, all species were collected and preserved in the author's private herbarium. Duplicates of the collections are on file at the Oregon State College Herbarium at Corvallis, Oregon.

In the rock-fell community studies the quadrat analysis method was used for determining dominance and successional trends. Growth-ring counts made from cores obtained by an increment borer were used in the study of relict species, in helping date the last forest fire, and as an aid in determining the relative stability of certain communities.

General Features of the Area

Topography and Geography.—The Monument Peak area consists essentially of two peaks connected by a high ridge and of two other ridges extending from the higher peak which in this study is designated New Monument. The

[1] The author wishes to acknowledge his appreciation to several individuals who have helped him with certain phases of the work: To my major professor, Dr. Helen Gilkey of Oregon State College, for her generous assistance and valuable suggestions on the problem as a whole and particularly on the taxonomic phase, to Dr. Henry P. Hansen of O.S.C. for suggestions and criticisms on the ecological phases of the work, to Professor Morton Peck of Willamette University, Dr. Philip Munz of the Rancho Santa Ana Botanic Garden, and Mrs. Harvey Hall for checking the author's determinations of special groups of species and to the New York Botanical Garden for the loan of 130 specimens of *Carex*.

second peak with an elevation of 4683 is referred to in this paper as Old Monument. Three ridges radiate from New Monument. One extends in a westerly direction, a second runs north, while the third bears southeast terminating in Old Monument. For convenience these are called West Ridge, North Ridge, and East Ridge respectively.

The region is characterized by mature topography and narrow V-shaped valleys. In comparison to the valley floor, which averages approximately 1000 feet, New Monument has an elevation of 4700 feet which is the highest relief in the general region. Its partially isolated position adds significance to a study of its flora.

Geology and Soils.—The Western Cascades in which Monument Peak is located have an average elevation of between 4500 and 5000 feet and have been folded to form gentle synclines and anticlines.

The rocks of the area are Oligocene-Miocene volcanics belonging to the Sardine formation which is composed principally of andesites and basalts characterized by their extreme resistance to erosion (Thayer, 1929).

The soils are mainly residual, shallow, including many rock outcrops, heavy in texture, and brown in color. (Kocher *et al.*, 1924). The soil depth varies from none on the ridges near the summit to two feet or more in the noble fir community. The edaphic factor, as will be pointed out later, is of major importance in controlling the distribution of tree species in the area.

Climate.—Monument Peak has a humid marine climate with the rainy season exceeding the dry period in length with the result that there is a moisture carry-over that supports a vegetation type with rather high moisture requirements and keeps the streams flowing the entire year. No weather data are available for the peak, consequently, it was necessary to interpolate temperature and precipitation from data recorded from three stations in the general region, one of the three being a mountain of similar elevation. The area lies between the 60 inch and 70 inch isohyetals (Stovall and Hopson, 1940). The summer rainfall is very light while approximately half the total precipitation falls during the three winter months principally in the form of snow. A shrub community on the south slope shows evidence of a heavy snow pack.

The growing season near the summit apparently averages approximately 3½ months with the snow usually disappearing early in June and the first killing frosts occuring in middle to late September.

Historical Factors.—Records of forest fires and logging operations are very meager, consequently information had to be gained from the people living in the area. The last fire in the area occurred near 1900 and burned the north and northeast slope only. There has been no extensive or significant logging during the past fifty years if ever. The area has had no grazing since 1908 and then for only one season.

VEGETATION

The Monument Peak area is in the Coast Forest Formation designated by Clements (1938) as the Cedar-Hemlock Association. However, cedar is almost entirely absent, being excluded apparently by altitude. It is replaced

by noble fir (*Abies procera* Rehd.) and lovely fir (*Abies amabilis* (Dougl.) Forbes). Douglas fir (*Pseudotsuga taxifolis* (Lambert) Britt.) and western white pine (*Pinus monticola* Dougl.) are also present but occupy areas from which the firs and hemlock are excluded by edaphic factors. Alaska cedar (*Chamaecyparis nootkatensis* (Lamb.) Spach.) and mountain hemlock (*Tsuga mertensiana* (Bong.) Sarg.) are found very sparingly here. The former is to be regarded as a relict species while the latter doubtless occurs here at the extreme lower limits of its range. A search on two other peaks within the same general area and with elevations between 4300 and 4400 feet failed to reveal either of these species. Although the area is primarily a forested one there are only eleven species of trees as compared to 41 shrubs and 219 species of herbaceous plants.

PLANT COMMUNITIES

Four major plant communities occur on Monument Peak. They are 1) a rock fell community, 2) the coniferous forests, 3) a shrub community, and 4) a bog-marsh. Some of these have geographic continuity while others consist of noncontiguous fragments. The coniferous forest considered as a unit is designated the Abies-Tsuga Association with three principal dominant species, namely western hemlock, noble fir and lovely fir. In this Association three rather distinct sub-divisions are recognized and treated separately. Reference to fig. 1 will show the geographic location of the various communities and their subdivisions.

THE ROCK-FELL COMMUNITY

Treeless areas occur at the summits and along the tops of the ridges. The absence of timber here is attributable to physiographic rather than to climatic factors. The largest single fragment of this disjunctive community is on West Hill at an elevation of about 4100 feet. The area comprises approximately

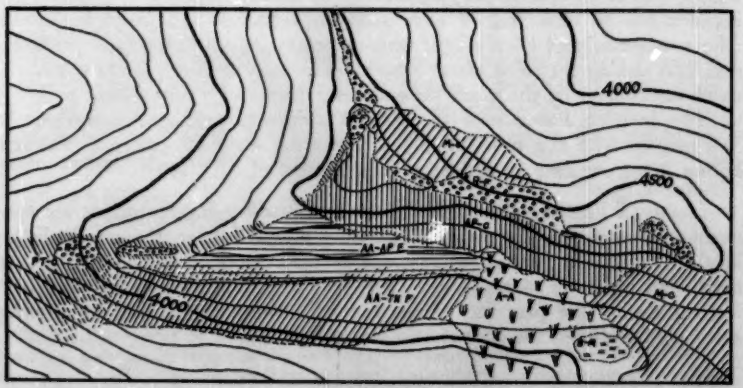

Fig. 1.—Plant communities on Monument Peak. AA-TH F—*Abies amabilis-Tsuga heterophylla* faciation; AP C—*Abies procera* consociation; AA-AP F—*Abies amabilis-A. procera* faciation; PT C—*Pseudotsuga taxifolia* consocies; R-F—Rock-fell; B-M—Bog-marsh; A-A—*Acer-Alnus;* M-C—Mixed conifer.

an acre. The portion characterized by rocky outcrops supports only a few lichens and other lithophytes, the most abundant of which are *Rhacomitrium lanuginosum* (Hedw.) Brid. and *Selaginella wallacei* Hieron. Areas covered by very shallow, gravelly soil supports certain chersophytes of which the following are most abundant: *Lomatium martindalei* C. & R., *Allium cascadense* Peck, *Erophyllum lanatum* (Pursh) Forbes, *Polygonum aviculare* L., *Microsteris gracilis* (Dougl.) Greene, *Festuca rubra* L., *Agrostis diegoensis* Vas., *Arctostaphylos nevadensis* Gray, *Montia parvifolia* (Moc.) Greene, *Saxifraga rufidula* (Small) Johns, and *Phlox diffusa* Benth. var. *longistylis* (Wher.) Peck.

The remaining portion of the hill is characterized by more nearly level areas covered by a mantle of soil thick enough to support a more or less complete plant cover in which psilophytes predominate. Typical species are: *Festuca rubra* L., *Agrostis diegoensis* Vas., *Luzula campestris* (L.) DC. var *multiflora* (Ehr.) Celak, *Fragaria platypetala* Rydb., *Erythronium oregonum* Appleg., and *Eriophyllum lanatum*.

Between this treeless island and the surrounding forest of western hemlock and Douglas fir is a narrow ecotone with the following typical species: *Penstemon nemorosus* (Dougl.) Trautv., *Lupinus latifolius* Agh. var. *subalpinus* (Piper and Robbins) C.P. Sm., *Amelanchier florida* Lindl., *Rubus parviflorus* Nutt., *Salix sitchensis* Sans., *Rhododendron macrophyllum* C. Don, and *Vaccinium membranaceum* Dougl.

That the rock-fell community is gradually shrinking is evidenced by the presence of seedlings and small trees of Douglas fir which are invading the margins.

Of particular interest was a single specimen of oak tentatively identified as Oregon white oak (*Quercus garryana* Dougl.) although its shrubby habit of growth hardly suggest this species. No fruit was found, consequently determination had to be made entirely on leaf characters. There are no other species of oak growing closer than 100 miles while the nearest white oak which the author could discover was at the base of the mountain some four or five miles distant and growing at an elevation of approximately 1000 feet. Oregon white oak in west central Oregon is ordinarily confined to elevations

Fig. 2—Rock-fell community at summit of New Monument with a pure stand of noble fir at left.

under 1500 feet and, in fact, is typically found below 1000 feet. The presence of this lone specimen at 4100 feet is best explained by regarding it as a relict of the post-glacial xerothermic period, the occurrence of which has been well established by several lines of investigation (Hansen, 1947) and (Hulten, 1937). During this period, between 4000 and 8000 years ago, oaks were probably common at elevations of 4000 feet. This species has persisted here because its coniferous competitors have found this micro-community too unfavorable to invade.

The other fragments of the rock-fell community though differing slightly in their exact floristic content are essentially similar ecologically. East Ridge is so rocky that only a few lithophytes are found near the top. The ecotone here and at the summit of New Monument separating the rock-fell community from the noble fir forest is sharp and characterized by western white pine and Douglas fir along with ocean spray (*Holodiscus discolor* (Pursh) Maxim) and service berry (*Amelanchier florida* Lindl.) as the principal shrubs.

Quadrat studies were made on West Hill and at the summit of New Monument to determine the dominant species. Various size quadrats from one quarter meter to four square meters were taken and a species area curve plotted (fig. 3). By inspection the one square meter was selected as the minimal size for accurate results. Forty-three quadrats were taken at intervals of from ten to fourteen yards. Five coverage classes were recognized as follows: Cover Class 1—1-5% coverage; Cover Class 2—6-25% coverage; Cover Class 3—26-50% coverage; Cover Class 4—51-75% coverage; and Cover Class 5—76-100% coverage.

Coverage data for the quadrats were obtained by estimations. In computing the mean coverage of a given species, the coverage percentages it possessed in the various quadrats were averaged. In making this computation the midpoint

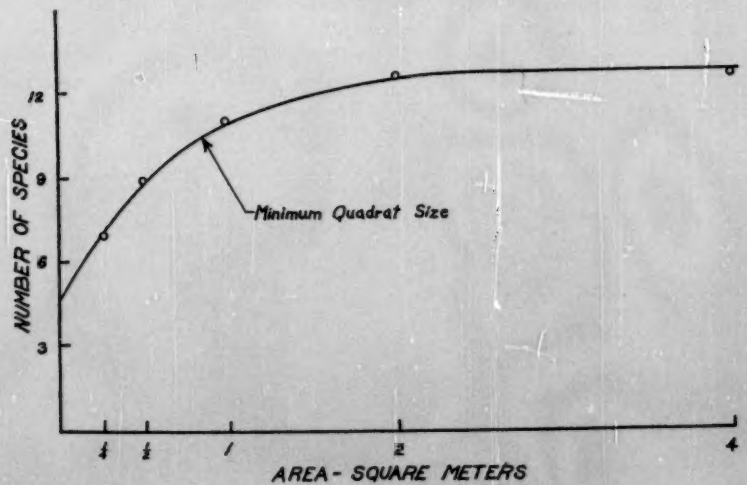

Fig. 3.—Species-area graph indicating the minimum quadrat size needed to sample the rock-fell vegetation.

in terms of percent in each class was arbitrarily used. For example, if *Eriophyllum lanatum* in quadrat 4 belonged to cover class 3, its coverage was figured at 38% in the averaging procedure.

Reference to table 1 shows the following seven species to be relatively high in both frequency and coverage: *Eriophyllum lanatum* 100% and 9%, *Rhacomitrium lanuginosum* 85% and 13%, *Festuca rubra* 80% and 9%, *Agrostis diegoensis* 80% and 7.5%, *Selaginella wallacei* 60% and 4.3%, *Polygonum aviculare* 75% and 1% and *Arctostaphylos nevadensis* 35% and 16%. They should all be regarded as seral dominants. As the shrub stage gradually replaces the herbaceous stage, it is to be expected that the frequency as well as the coverage of *Arctostaphylos nevadensis* will increase.

Reference to table 2 shows that six of the above species are relatively high in frequency and coverage in the rock-fell area at the summit of *New Monument*. The exception is *Arctostaphylos nevadensis* which is replaced by *A. uva-ursi*. By way of contrast the number of species at the summit is con-

TABLE 1.—Frequency and coverage data for West Hill

Species	Coverage %	Frequency %
Eriophyllum lanatum	100	9
Rhacomitrium lanuginosum	85	13
Festuca rubra	80	9
Agrostis diegoensis	80	7.5
Polygonum aviculare	75	1.0
Castilleja hispida	70	1.4
Calochortus lobbii	65	2.0
Selaginella wallacei	60	4.3
Lomatium martindalei	60	1.8
Saxifraga rufidula	55	1.0
Montia parvifolia	55	1.0
Sedum spathulifolium	40	1.2
Phlox diffusa var. longistylis	40	3.7
Allium cascadense	40	1.2
Comandra umbellata	40	1.0
Arctostaphylos nevadensis	35	16.0
Microsteris gracilis	25	.75
Saxifraga ferruginea	20	.6
Luzula campestis	20	.6
Cryptogramma acrostichoides	15	.45
Orobanche uniflora	10	.3
Xerophyllum tenax	10	.3
Polytrichum juniperinum	5	.15
Erythronium oregonum	5	.15
Achillea lanulosa	5	.8
Delphinium menziesii	5	.15
Juniperus sibirica	5	1.0
Pseudotsuga taxifolia (seeding)	5	.15

Other species in this Rock-Fell Community not obtained in the quadrats:

Quercus garryana
Castilleja miniata
Hieracium albiflorum
Lilium columbianum
Penstemon nemorosus
Epilobium lactiflorum
Rhododendron macrophyllum
Antennaria concolor
Carex inops

TABLE 2.—Frequency and coverage data for the rock-fell community at the summit of New Monument

Species	Frequency %	Coverage %
Festuca rubra	90	14.3
Eriophyllum lanatum	90	9
Penstemon procerus	65	4.5
Selaginella wallacei	60	2.5
Calochortus lobbii	60	1.8
Rhacomitrium lanuginosum	60	10.4
Lomatium martindalei	60	1.8
Agrostis diegoensis	45	3.7
Polytrichum juniperinum	40	1.2
Saxifraga rufidula	40	1.2
Arctostaphylos uva-ursi	40	10
Achillea lanulosa	40	2.5
Polygonum aviculare	40	1.2
Castilleja hispida	35	1
Sedum spathulifolium	30	.9
Comandra umbellata	25	.75
Rosa spaldingii	25	1.4
Zygadenus venenosus	25	.75
Silene douglasii	25	.75
Cryptograma acrostichoides	25	.75
Luzula campestris	25	.75
Erythronium grandiflorum var. pallidum	15	.45
Heuchera micrantha var. pacifica	15	.45
Antennaria concolor	10	3.8
(An unidentified crustose lichen)	10	.3
Hieracium albiflorum	10	1
Fragaria platypetala	10	.3
Gilia capitata	10	.3
Juniperus sibirica	10	9
Pachystima myrsinites	10	.3
Hemizonella minima	10	.3
Penstemon cardwellii	10	2.0
Orthocarpus imbricatus	10	.3
Epilobium angustifolium	5	.15
Anemone oregana	5	.15
Mimulus breweri	5	.15
Lupinus latifolius var. subalpinus	5	.15
Allium cascadense	5	.15
Habenaria saccata	5	.15
Montia parviflora	5	.15
Carex inops	5	.15
Juncus effusus	5	.15
Sedum divergens	5	.15
Berberis aquifolia	5	.15
Potentilla glandulosa	5	.15
Ceanothus velutinus	5	.8
Penstemon serrulatus	5	.15
Anaphalis margaritacea	5	.15

Other species in the community but not obtained in the quadrats:

Hieracium chapacanum
Penstemon rupicola
Collinsia parviflora
Erysimum asperum
Rumex acetosella
Arenaria macrophylla
Delphinium menziesii
Eriogonum umbellatum
Saxifraga bronchialis var. austromontana
Saxifraga ferruginea
Xerophyllum tenax
Rubus lasiococcus
Lilium washingtonianum
Polygonum bistortoides
Chamaecyparis nootkatensis
Tsuga mertensiana
Poa secunda
Danthonia intermedia
Festuca occidentalis
Trisetum canescens
Elymus glaucus
Carex rossii
Juncus parryi

siderably greater than on West Hill. Only two species of grass are found in the former area while the summit produces seven. A greater soil depth and a consequent slight amelioration of the habitat from the standpoint of water relations is reflected by the floristic differences.

CONIFEROUS FOREST COMMUNITIES

Abies procera Community.—Bordering the rock-fell community (except the West Hill fragment) is a forest band consisting of a nearly pure stand of noble fir. The vertical extent of this forest is approximately 300 feet beginning at about 4300 feet and disappearing at roughly 4600 feet. Its upper limit is controlled by edaphic factors and where the latter are favorable, as near both summits, noble fir reaches to nearly 4700 feet. The north slope of East Ridge is too precipitous to support any tree growth above 4400 feet. Below that elevation a mixed stand of young trees occurs, probably representing the new growth which followed the Rock Creek fire. North Ridge was not studied in detail but the noble fir there too is confined largely to elevations below 4500 feet because of the physiographic factors. The north slope of West Ridge supports a rather large stand of even growth noble fir (see fig. 4).

The trees in this community are typically so close together as to make the forest floor very dark. Consequently there are very few associated species. A shrub layer is entirely absent except where an opening in the canopy occurs. Two ericads, *Chimaphila menziesii* (R. Br.) Spreng., and *Pleuricospora*

Fig. 4.—Noble fir community at 4600 ft. This is a closed forest with a striking dearth of vegetation on the forest floor.

fimbriolata Gray, the latter almost entirely hypogenous, together with *Asarum caudatum* Lindl. are found in the dense forest; while *Pyrola dentata* Smith, *Collinsia grandiflora* Dougl., *Symphoricarpos mollis* Nutt., *Smilacina sessilifolia* Nutt., *Clintonia unilfora* Kunth, *Anemone deltoidea* Hook., *Polemonium carneum* Gray, *Rosa gymnocarpa* Nutt., *Ribes viscossimum* Pursh, and *Rubus parviflorus* Nutt. are typical species along the margins and in small clearings. *Pleuricospora fimbriolata* has a very high fidelity for this habitat. It may be said to be an exclusive for the dark floor of the noble fir community.

Noble fir although a main component of the forest on the west slope of the Cascade Range in Washington and Oregon between 3000 and 5000 feet according to Hanzlick (1925) rarely occurs in pure stands as it does on Monument. It is a tree of intermediate tolerance, (Baker, 1934) similar in this character to Douglas fir but less tolerant than western hemlock and western red cedar.

Increment cores taken from specimens on Monument Peak revealed the pure stand to be of uniform age and approximately 46 or 47 years old. According to a local long-time resident, Mr. L. T. Hennis, a forest fire burned across a part of this area at about the year 1900. The age of the stand would corroborate the testimony of Mr. Hennis. The lower margin of this stand meets the shrub community in an alterne; a transition zone is entirely lacking.

An effort was made to see whethere the boundary between those two adjacent communities is static or whether one community might be encroaching upon the other. The increment cores showed that the fir trees along the margin next to the alder-maple community are the same age as those located further in the fir stand. A careful search revealed no seedlings of species of either community along the border. Furthermore, since all three species involved are only moderately tolerant, it is concluded that the border between the two communities is quite static. Along the upper margin of the noble fir community where it meets the rock-fell community there is a narrow ecotone with service berry and ocean spray as typical shrub species and with scattered specimens of western white pine and Douglas fir. The former find the ecotone region favorable because of the protection from the wind afforded by the forest combined with a greater amount of light. The two tree species are able to establish themselves on soil that is too rocky for noble fir.

Abies amabilis-Tsuga heterophylla Community.—This community reaches its best development on the southwest slope of New Monument between 4000 and 4400 feet. The hemlock trees outnumber the firs nearly three to one and average somewhat larger with many individuals attaining a trunk diameter of from three to four feet, while very large specimens of lovely fir but rarely occur.

There is evidence of some reproduction by both species. Because of the rather open canopy there exist three rather distinct though discontinuous layer societies. There are the tall shrub layer consisting of *Acer circinatum* and *Sambucus callicarpa;* the low shrub layer composed of *Ribes lacustre, R. viscosissimum, Rosa gymnocarpa* and *Rubus parviflorus* (this species especially abundant in the clearings); and the herbaceous layer. A list of the species found in the last society follows below.

Pteridium aquilinum var. *lanuginosum*
Polystichum munitum
Melica smithii
Melica subulata
Trillium ovatum
Luzula parviflorus
Smilacina sessilifolia
Streptopus amplexifolius
Oxalis oregana
Cornus canadensis
Montia sibirica
Achlys triphylla
Galium triflorum
Galium oreganum
Viola glabella
Tiarella unifoliata
Epilobium angustifolium
Thalictrum occidentale
Anemone deltoidea
Dicentra formosa
Valeriana sitchensis
Hydrophyllum tenuipes

Abies procera-Abies amabilis Community.—At about 4300 feet the hemlock is replaced by noble fir. This division of the association differs from the previous one in that the forest floor is only sparsely covered with vegetation and that it possesses a slightly different floristic composition. Species found in the noble fir-lovely fir community not found in the previous community are as follows:

Xerophyllum tenax
Pyrola dentata
Rubus lasiococcus
Vaccinium membranaceum
Polemonium carneum
Symphoricarpos mollis

The soil throughout the area occupied by the firs and hemlock is medium to shallow with occasional exposed rock. There is a considerable amount of humus in the A-horizon and the soil gives evidence of being quite fertile.

Pseudotsuga taxifolia Community.—Douglas fir spreads over the north, west, and south slopes of West Hill and extends as a narrow interrupted corridor up the rise to the summit of New Monument. Owing to its more xeromorphic character this tree has been able to establish itself on the soil that is too dry and rocky for hemlock and true fir. Below 4000 feet where it occurs as a nearly pure stand made up of medium-sized trees, there is evidence that the absence of the hemlock is temporary and can be attributed to recent fires.

Oxalis oregana, creates an aspect society on the forest floor on the west slope below 4000 feet. *Vancouveria hexandra* (Hook.) Moor. and Dene. is apparently restricted to this locality.

THE SHRUB COMMUNITY

This community, (fig. 5) dominated by vine maple and Sitka alder, is confined to a moderate southwest slope characterized by an abundance of soil moisture. Its replacing the noble fir forest so abruptly at about 4300 feet poses an interesting problem. Investigation revealed that soil differences in the two communities are not significant. The same kind of parent rock underlies both areas and only slight differences occur in the soil depth. According to an old resident, the maple-alder stand has occupied approximately its present position at least since 1864. Ring growth counts revealed the average age of the alders to be between 50 and 55 years with one specimen reaching the age of 70. The maples averaged just slightly younger although the small difference might be apparent rather than real produced by the method of sampling. The basal portions of the trunks of most of both maples and alders are prone and recline down the slope. The heavy snow pack of the winter is probably the chief factor responsible for this phenomenon.

Fig. 5.—*Acer-Alnus* associes. No tension zone occurs between this community and the adjacent coniferous forest.

This community is apparently heavily populated by mountain beaver. Evidence of co-action between this rodent and the vegetation as a factor in the occurrence of two distinct but contiguous and stable communities was sought but with negative results. This animal feeds on a great variety of plants but Bailey (1936) reports that he did not find where they injured any number of large or small conifers.

The occurrence of the alder-maple community is to be explained on the basis of several factors. First, the terrain occupied by this stand is less steep than the adjacent slope covered with fir. Second, the soil moisture content during the growing season is higher owing to seepage except for islands with drier soil that support only herbs. Finally the stand of vegetation is so dense that the chance is slight that even a highly tolerant conifer seedling could establish itself. A profile of the southwest slope from the top of East Ridge to the 4000 feet contour showing the slope relationships of four adjacent communities is found in fig. 6.

There is no evidence of fires having disturbed the area recently. However, one very old snag, apparently a conifer, does occur in the midst of the shrubs. Presumably the area at one time supported a coniferous forest and during that time soil conditions were improved. When the conifers were removed by

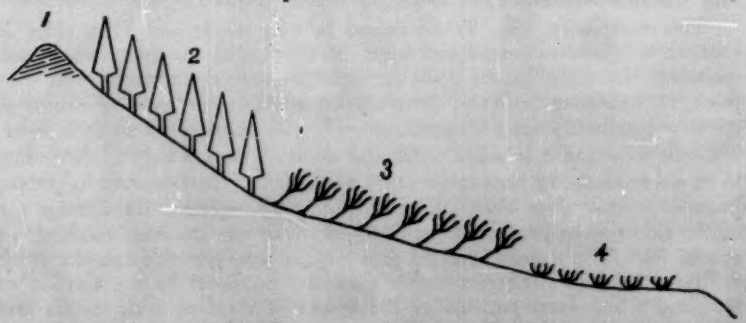

Fig. 6.—Profile of south slope of east ridge: 1. Rock-fell community, 2. Noble fir community, 3. Alder-maple community, 4. Bog-marsh community.

some kind of disturbance, the shrubs became established and it seems likely that they may hold the area against invaders until the habitat becomes more xeric through better drainage or until a disturbance removes the alder and maple.

Although maple and alder are found together in much of the area, in some places they occur separately with the latter showing a preference for the wetter portions of the community. Typical associate species of alder when it occurs without maple are *Athyrium Felix-femina, Trillium ovatum, Smilacina sessilifolia, Streptopus amplexifolius, Montia sibirica, Dicentra formosa, Tolmiea Menziesii,* and *Viola glabella.* Typical plants in the maple consocies are *Hydrophyllum tenuipes* and *Actaea arguta.*

Four rather well-defined layer societies are found in this community. The first which may be designated as the tall shrub synusia consists principally of the two seral dominants, *Alnus sinuata* and *Acer circinatum* with *Salix sitchensis* and *Prunus emarginata* var, *erecta* occasionally present.

The second synusia or lower shrub society may include all or most of the following. *Sambucus callicarpa, Rubus spectabilis, Oplopanax horridum* and *Ribes bracteosum.* A tall herbaceous stratum most marked in the drier areas during the latter part of the growing season is composed of the following species:

Senecio triangularis
Mertensia paniculata var. *borealis*
Heracleum lanatum
Thalictrum occidentale
Rudbeckia occidentalis
Stachys ciliata
Actaea arguta

A low herb synusia is easily discernible with the following species typically present:

Viola glabella
Synthyris reniformis
Disporum oreganum
Luzula campestris
Montia sibirica
Tolmiea menziesii
Smilacina sessilifolia
Carex festivella
Rumex acetosella
Boykinia major
Osmorhiza nuda
Stachys rigida
Achillea lanulosa

THE BOG-MARSH COMMUNITY

At approximately 4000 feet elevation on a southwest slope immediately adjacent to the shrub community is an area characterized by soil that is nearly to entirely saturated throughout the growing season. Two other very small marshy areas at between 4300 and 4400 feet contribute a few additional species of bog and/or marsh plants so their flora will be considered along with that of the main bog. Hydrarch succession is occurring in this community although the seral stages are not sharply differentiated.
Growing in the wetter areas are:

Sphagnum
Cardamine breweri var. *orbicularis*
Lysichitum americanum
Scirpus congdoni
Habenaria leucostachys
Montia cordifolia
Ranunculus populago
Caltha biflora
Parnassia intermedia
Hypericum anagalloides
Epilobium glandulosum
Veronica americana
Mimulus moschatus
Galium cymosus

In the more mesic zones of the community species of grasses and sedges predominate; not, however, to the exclusion of certain forbs. The following are the most characteristic species.

Glyceria leptostachya
G. elata
Pleuropogon refractus
Calamagrostis canadensis
Agrostis thurberiana
Carex mertensii
C. kelloggii
Habenaria saccata
Montia sibirica
Achillea lanulosa
Carex festivella
Aconitum howellii
Thalictrum occidentalis
Spiraea densiflora
Viola macloskeyi
Osmorhiza occidentalis
Heracleum lanatum
Vaccinium ovalifolium
Veronica humifusa
Arnica latifolia
Senecio triangularis

At the summit of New Monument is a small group of Alaska cedar (*Chamaecyparis nootkatensis*) and mountain hemlock (*Tsuga mertensiana*) constituting what may be regarded here as a faciation of the Tsuga-Abies Association. There is one clump of Alaska cedar where eight large trees arise from what appears to be a common woody base. Typically the boles of Alaska cedars exhibit broad, buttressed, and often fluted bases (Harlow and Harrar, 1941). Whether this represents suckering, a phenomenon unknown among conifers except in Sequoias, or a coalescence of the bases of several trunks the author was unable to determine. Increment cores taken from the trees in the clump indicated an age span of from 150 to over 300 years.

PLANT SUCCESSION

If the traditional view of plant succession is accepted, several xerarch stages could be recognized. Some of the rocky outcrops are covered with crustose lichens while others have had sufficient soil formed on their surfaces to support certain carpet mosses such as *Rhacomitrium lanuginosum* and *Polytrichum juniperinum* and the club moss, *Selaginella wallacei*. Rooting in the crevices are *Sedum spathulifolium* and *Saxifraga rufidula*. Two small annuals, *Polygonum aviculare* and *Gilia capitata* along with certain perennials such as *Phlox diffusa* var. *longistylis*, *Heuchera micrantha* var. *pacifica*, and *Montia parvifolia* are the next to appear. As a little more soil accumulates *Eriophyllum lanatum*, *Lomatium martindalei*, *Allium cascadense*, *Festuca rubra*, *Agrostis diegoensis*, *Castilleja hispida* and *Calochortus lobbii* take over the space. Surrounding the xerophytic community is an ecotone composed of more mesic herbs and certain shrubs. The following are typical: *Penstemon nemorosus*, *Lupinus latifolius* var. *subalpinus*, *Lilium columbianum*, *Xerophyllum tenax*, *Rhododendron macrophyllum*, *Vaccinium membranaceum*, *Berberis nervosa* and *Amelanchier florida*.

Beyond the shrub ecotone is the forest with the more xerophytic Douglas fir encountered first followed by western hemlock. Xerarch succession follows essentially the same pattern at the summit of New Monument except that noble fir replaces western hemlock as the principal dominant, while western white pine and ocean spray are commonly found in the ecotone between the rock-fell and forest communities. Also Alaska cedar and mountain hemlock occur here though sparingly, and according to the Clementian view both would be regarded as climax dominants.

In the bog-marsh community the submerged stage is represented by *Cardamine breweri* var. *orbicularis*. A bog stage is represented by Sphagnum moss and skunk cabbage (*Lysichitum americanum*). The sedge-grass stage is represented by five species of grasses and three of *Carex* besides several moderately hydrophytic forbs. This area shades gradually into the shrub zone and is evidently being invaded by the latter.

LIFE ZONES

There is apparently a unanimity of opinion among plant ecologists of the Cascades in recognizing western hemlock, western white pine, lovely fir and noble fir as four of the most characteristic trees of the Canadian Life Zone. These four species with Douglas fir account for most of the forest area of Monument Peak. Bailey (1936) excludes noble fir from and includes Alaska cedar in his list of Canadian Zone indicator trees, while Peck (1941) regards Alaska cedar as characteristic of the Hudsonian. Mountain hemlock, found sparingly at the summit, is usually regarded as Hudsonian.

Monument has five of the six species of shrubs which Jones (1938) lists as characteristic of the Canadian Zone of Mt. Rainier. On the basis of the trees and shrubs present the area is predominantly Canadian Life Zone.

The biological spectrum according to Raunkiaer (1934) was worked out for Monument Peak. It is listed below along with the spectra from the Canadian and Hudsonian zones from Mt. Rainier and the Olympic Peninsula. It will be seen that the percentages for the various categories on Monument correspond more closely to those of the Canadian zones of Rainier and the Olympic Peninsula than to those of the Hudsonian zones of the two regions. This fact verifies the conclusion that Monument is Canadian Life Zone.

Region	Percentage of Species				
	Ph*	Ch	H	Cr	Th
Mt. Rainier-Canadian Zone	11	8.0	47	31	3
Olympic Peninsula-Canadian Zone	12	8.0	49	31	1
Monument Peak	12.4	8.0	53	21	5.6
Mt. Rainier-Hudsonian Zone	9	14	61	13	1
Olympic Peninsula-Hudsonian Zone	9	10	67	13	1
Normal World Spectrum	46	9	26	6	13

* Ph—Phanerophytes, Ch—Chamaephytes, H—Hemicryptophytes, Cr—Cryptophytes, Th—Therophytes.

It will be noted that the percentage of therophytes for Monument Peak is higher than for either Mt. Rainier or the Olympic Peninsula. This is attributable to the considerable number of introduced weedy ruderals on Monument.

THE GEOGRAPHICAL AFFINITIES OF THE FLORA

The vascular flora of that part of Monument Peak included in this study comprises 280 species and varieties of which 261 are indigenous (table 3). The affinities of some of these species are quite clear while with others the relationships cannot be definitely established with our present information.

Of the total number of species found on Monument above 3600, 91 are listed by Hulten (1937) as boreal. Raup (1947) adds two to the list, while Campbell and Wiggins (1947) include five additional making a grand total

TABLE 3.—Geographical distribution of the species comprising the present flora at Monument Peak.

Areas covered by known distribution	Number of species	Percentage of total flora
Pacific Region primarily west of Sierra-Cascades	121	43.0
Pacific Region and Rocky Mountains	48	16.8
Oregon northward	42	16.0
All North America	21	7.5
Eastern Oregon and eastward	8	2.9
Oregon to California	7	2.5
Limited to Oregon	6	2.14
Pacific Region to North Central N.A.	6	2.14
Northern North America	2	0.07
Introduced from various regions	19	6.8

of 98 species or approximately 35% of the total. Approximately two thirds of this group are believed to have had their center of distribution in Southern Beringia, an area which escaped Pleistocene glaciation, and to have spread south and east. Another group, circumpolar in their present distribution, are believed to have survived chiefly south of the ice during Pleistocene times. They were not depauperated of biotypes and therefore have retained their ability to spread. Of the thirteen species on Monument belonging to this group, nine range over the mountainous region of the entire North American Continent. There is another group of species which range eastward and southward. Too little is positively known about their centers of dispersal to warrant assigning them to definite categories based on origin. It is likely that certain of them should be classed with Abrams Mexican element as they are xerophytic and range principally southward on the east side of the Sierra-Cascade Range.

The continental distribution of all the species on Monument Peak is given above. It is significant that there are on Monument Peak six times as many species which range from Oregon northward through Washington or farther as are limited to Oregon and California. Northwest Oregon has more in common climatically with the region to the north than it has with the area to the south. The Rogue River region of Southern Oregon is believed to constitute a barrier to the north-south migration of certain species.

Adventives.—Although the area is somewhat remote from human communities, 6.8 percent of the species are introduced. Of the nineteen adventives, three are grasses, one is a shrub, Scotch broom, while the remaining fifteen are forbs six of which are from the Compositae family.

Poa pratensis
Phleum pratense
Dactylis glomerata
Rumex acetosella
Polygonum aviculare
Spergularia rubra
Cytisus scoparius
Trifolium pratense
T. repens
Hypericum perforatum
Prunella vulgaris
Plantago major
Anthemis cotula
Cirsium lanceolata
C. arvense
Taraxacum officinale
Hypochaeris radicata
Chrysanthemum leucanthemum var. *pinnatifidum*

Relicts and Species with Discontinuous Distribution.—Antennaria concolor which ranges from northern Linn County, Oregon to southwestern Washington should be regarded as an endemic. Until recently discovered in southern Lane County, Oregon, *Allium cascadense* should have been regarded as an endemic restricted to a small area in northeast Linn County, but this new location for it suggests that it is a disjunct. However, intensive collecting between the two areas might show a rather continuous distribution.

Stellaria obtusa, according to Jones (1936) has not been reported in Washington except from the Olympic Peninsula, and prior to this study it was thought to be limited to northeastern Oregon. Since *Stellaria* is regarded as a genus of northern origin, it is probable that *S. obtusa* is a relict species on Monument Peak driven south by Pleistocene glaciation but with the return of warmer, drier conditions have disappeared except in a few isolated refugia at rather high altitudes. *Chamaecyparis nootkatensis* with a discontinuous distribution in northern Oregon has undoubtedly had a similar history. *Carex festivella* according to the literature is restricted to the east slope of the Cascades except for a recent report from southern Lane County by Baker.

Ranunculus populago and *Fragaria platipetala* although listed in the floras of Oregon as limited to the east slope of the Cascades, occur on Monument. Both have been collected by the author some twenty-five miles south of Monument at Tombstone Prairie which is also on the west slope of the Cascades.

It is significant that of the 17 species whose known ranges have been extended by this study, in 15 cases the extension has been westward, that is, across the summit of the Cascade Mountains. This could mean one of three things. First, it can be assumed that these species are of polyphyletic origin evolving on opposite sides of the Cascade barrier. This hypothesis is, however, very unlikely since no morphological differences between the representatives from opposite sides of the mountain were detected.

A scond explanation is that these species occurred over most of the state before the Cascades arose to their present height and are therefore very old. Such remarkable stability of species to make this hypothesis tenable is highly unlikly particularly in herbaceous forms. Therefore, this explanation is not offered as the solution.

The third possibility is that these particular species have not found the high mountain range to be an insurmountable barrier and therefore have migrated across in rather recent times. This hypothesis in the opinion of the author is the most feasible one of the three. It is between 8000 and 4000 years ago since the Cascade mountains probably presented a less formidable barrier then with less snow and a longer growing season near the summit than at present.

PERIODICITY DATA FOR 1948

An attempt was made to note at intervals of approximately two weeks all the species which were in flower. Data were obtained for 224 species. A horizontal block graph was constructed to show the results. It will be noted from fig. 7 that there were two peaks giving a bimodal curve. The first was in late June and the second during the latter part of July. The differences in dates of flowering of a given species with different altitudes was negligible.

Montia sibirica which was found in flower at every check date from May 24 to September, had the longest continuous flowering period. *Dicentra formosa, Erysimum asperum, Tiarella unifoliata* and *Microsteris gracilis* flowered continuously from June 17 to September 13.

SUMMARY

Monument Peak is located on the west flank of the Cascade Range in Northern Linn County, Oregon. The area lies within the cedar-hemlock division of the coast forest formation. The principal dominants of the coniferous communities are *Tsuga heterophylla, Abies amabilis,* and *Abies procera* with *Pseudotsuga taxifolia* and *Pinus monticola* occurring in areas with slightly less favorable edaphic conditions. *Thuja plicata* is restricted to elevations below 4000 feet while *Tsuga mertensiana,* found sparingly at the summit, should be regarded as a co-dominant and occurs here at the extreme lower limits of its range.

Collections over two summers (1947 and 1948) from 3700 feet to the summit (4700 feet) yielded 280 species and varieties of vascular plants. Above 4000 feet the flora is quite typically Canadian with a few characteristic Hudsonian species such as *Chamacyparis nootkatensis* and *Tsuga mertensiana.* The climate is hemicryptophytic. The biological spectrum corresponds very closely to those of the Canadian zones of Mt. Rainier and the Olympic Peninsula.

Four distinct plant communities are found in the region; a rock-fell, a coniferous forest, a deciduous shrub, and a bog-marsh community. On dry,

EXTENSIONS OF RANGE

Species	Direction of Extension	Former known limits of Range
Melica smithii	W	SE Washington and NE Oregon
Poa canbyi	W	E Washington and E Oregon
Poa secunda	W	E and S Oregon
Carex festivella	W	Blue Mts. of Oregon
Scirpus congdoni	N	Josephine Co. to McKenzie Pass
Allium cascadense	W	Jefferson Park, Linn Co.
Stellaria obtusa	W	NE Oregon and Olympic Peninsula
Erysimum asperum	W	East of Cascades
Arabis holboelii var. secunda	W	East slope of Cascades and Eastern California
Sedum divergens	W	East slope of Cascades
Fragaria platypetala	W	East slope of Cascades
Rosa spaldingii	W	East of Cascade summit
Epilobium adenocaulon var perplexans	W	E Washington to E California
Gayophtum humile	W	East slopes of Cascades
Orogenia fusiformis	N	California and SW Oregon
Mimulus breweri	W	NW Oregon
Ranunculus populago	N & W	Blue Mts. and the Cascades from California to McKenzie Pass, Oregon

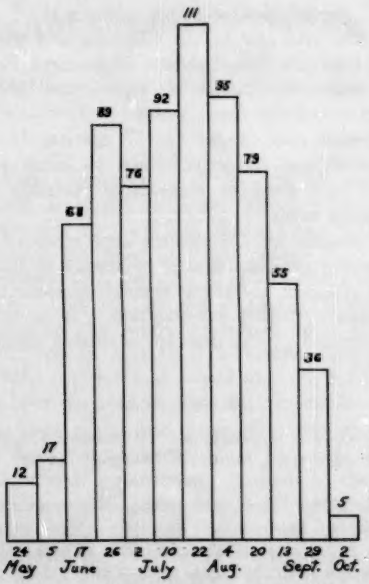

Fig. 7.—Histogram showing the number of species in flower at the check dates.

rocky west slopes a distinct flora ranging from lichens and mosses to grasses, annual and perennial forbes all with xerophytic affinities occurs. Quadrat studies revealed three important seral dominants: *Eriophyllum lanatum, Rhacomitrium lanuginosum* and *Festuca rubra*. Rather poorly defined stages in hydrarch succession were noted in the bog-marsh community. A relatively stable *Alnus sinuata-Acer circinatum* associes covers a large southwest slope. There is evidence that the community has existed in the area for quite a long time and is apparently holding its own against the climax dominants of the region. The persistence of this community is to be explained in part by a time-place factor. These species apparently became established after some catastrophe had destroyed the climax forest. Seepage keeps the soil very wet promoting thick, rank growth of the seral dominants and thus helps prevent invasion by the climax dominants.

A single specimen of dwarfed *Quercus garryana* found at 4000 feet doubtless is a relict from a dry period shown by various investigators to have occurred between 8000 and 4000 years ago. Alaska cedar is likewise to be regarded as a relict exhibiting, as it does, a discontinuous distribution. There is some evidence that one clump of this species has arisen through suckering from a parent tree.

Thirty-five percent of the species found on Monument Peak are known to be of boreal origin, and it is likely that quite a number of additional species migrated to the area from the north. A small number of the species

probably belong to the Mexican element while a third group is believed to have originated in the area east of the Cascades and the Great Basin. One or two endemic species are found in the Monument Peak area and several forms with discontinuous distribution are represented here. Adventive species account for 6.8 percent of the flora..

The study revealed new ranges for 17 species, 13 of which, according to the literature, were not formerly known to occur west of the Cascade divide. It is held that most of these have probably migrated across the Cascades within reecnt times.

The flowering periods of 224 species were recorded for the summer of 1948. July 22 saw the greatest number of species in bloom—a total of 111.

The taxonomic phase of the study opened up some new problems in this field which will require further investigation. It is believed, for example, that additional study may yield new and valuable diagnostic characters for one section of *Carex*.

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The Vegetation of Voorhees State Park, New Jersey

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Voorhees State Park, consisting of 534 acres of woodand, old fields, conifer plantations, and developed recreation areas, is located in Hunterdon County along the west side of the High Bridge-Long Valley road, approximately one mile north of the town of High Bridge (fig. 1). Four-fifths of the present park property was the gift of Foster M. Voorhees, a former governor of the state. This was in two sections, Hoppock Grove on the north, and Hill Acres on the south, making a total of 429 acres. The middle tract, consisting of an additional 105 acres bisected by the central stream, was subsequently acquired and served to unite the properties.

The land having been donated to the state for conservational and public recreational purposes, a program with these objectives in view was initiated in 1929. Intensive development began in 1932 when the state, with the co-operation of the federal government, undertook the establishment of varied recreational facilities within the park. Campfire and picnic sites, trails and shelters were constructed, chiefly in the northern or Hoppock Grove section, and to a less extent in the southern or Hill Acres section. The conifer plantations were also established at this time, on abandoned fields and in old

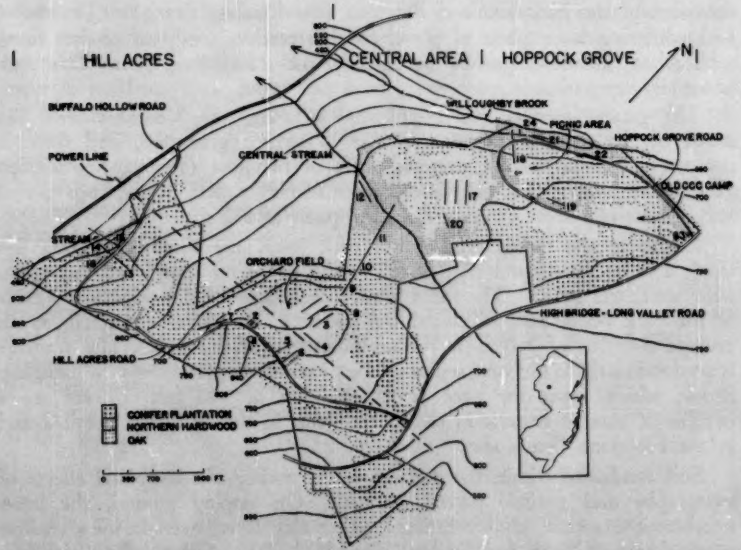

Fig. 1.—Outline map of Voorhees State Park indicating prominent features, distribution of principal communities, and location of transects used in the collection of data.

orchards. Technical supervision was provided by the National Park Service, their objective being to make the area available for the fullest public use, and at the same time to preserve and protect the natural resources (U.S. Department of Interior, 1937).

The vegetation of Voorhees Park has been through a long period of disturbance since settlement, at first through use as a farm, including its woodlot. Later, through the activities of the Civilian Conservation Corps in their initial work of developing the park, interference with the natural vegetation continued to some extent. However, there is no indication that any major disturbance of the vegetation has occurred within the park since the completion of this latter work. In recent years, a number of the park facilities have deteriorated to the extent that they have been removed or fallen into disuse. The level of maintenance has not been adequate to keep the park as it was originally developed.

Thus the situation within the park is now found to be one in which the natural plant cover has been provided with the freedom to reestablish itself over much of the area. This combination of circumstances offered an opportunity to make a study of the reemergence of a natural vegetation in this particular section of North Jersey.

The park lies within a physiographic division of the state referred to as the Jersey Highlands, a 900 square mile area with an average elevation of 1000 feet. It consists of a series of ridges and intervening valleys with a pronounced NE-SW trend, the whole extending across the northern part of the state (Kummel, 1940). Geologically, the area is considered to be an extension of the New England Province (the Reading Prong). The native rock, differing from place to place, consists predominantly of gneiss, along with schist, intrusive igneous (gneissoid) rock, and limestone. The park is entirely on gneiss.

The greater part of the Highlands, including the Voorhees area, lies south of the terminal moraine of the Wisconsin glaciation, and there is present only some widely scattered drift of previous (Jerseyan) glaciation (Salisbury, 1902). The drift is composed of native rock, having been carried only a relatively short distance from the point of origin.

Regarding the topography of the park itself, the southern portion lies along a ridge (maximum el. 840 ft.) which drops off sharply to the northwest, west, and south. The main south-facing slope of the ridge lies outside of the park boundaries. Toward the northeast the slope is gradual, to an average elevation of 740 ft. at the northeast end of the park. The drainage is predominantly to the west and southwest into the largest stream, Willoughby Brook, which leaves the park at an elevation of 540 feet. There are a number of smaller streams in the central area, in the southwest portion, and in the Hoppock Grove area.

Soil conditions within the park represent mainly the combined effects of topography and gneissic parent material. On sloping ground, the latter weathers into a thin, undifferentiated, gritty clay layer, overlain by a shallow accumulation of litter and humus (Patrick, 1920). Stones of all sizes are abundant. Erosion on the slopes appears to have resulted in a somewhat thicker soil layer on the lower ground. Also, during the time of the Wis-

consin glaciation, solifluction must have contributed appreciably to the soils now found at the base of the steep slopes (Denny, 1951).

Records taken at the nearest weather bureau station, Flemington, are suggestive of the general climatic conditions that prevail in the area. Records show average January-July temperatures of 30.8° and 74.8° F, with extremes of —18° and 108° F, an average growing season of 180 days, and an average annual precipitation of 44 inches (U.S. Dept. of Agr., 1941).

The deciduous forests of eastern United States have been the object of extensive studies by a number of workers and, in a general way, are quite well known. To consider only some of the work done in this immediate region: Bray (1930), in New York State, saw here an indefinitely delimited transition or tension zone between the oak-hickory forests to the south of this region, and the hemlock-hardwood to the north. This hemlock-hardwood forest type, in Connecticut, has been described in detail by Nichols (1913), among others. Raup (1938), in the Hudson Highlands of New York, recognized several forest types with regional affinities that were locally segregated according to the topography—the mesic and northern cove hardwoods, the xeric and western oak-hickory, and the southern chestnut oak-chestnut. Niering (1953), in an area of varied topography (High Point State Park, Sussex Co. N.J.) in the Ridge-Valley Province, was able to delimit a number of communities, the chestnut oak being most extensive. Cantlon (1953) investigated the effects of microclimatic conditions on the distribution of plant species on a diabase ridge located within a few miles of the Voorhees area. Chestnut oak (*Quercus prinus*), red oak (*Q. rubra*), black oak (*Q. velutina*), and sweet birch (*Betula lenta*) were observed to have the greatest basal area values, with pronounced differences in the proportion of each on the north as compared with the south slope. The composition of the tree cover in northern New Jersey has been given from the forester's viewpoint by Moore (1939) as mixed hardwood-oak, with subordinate maple, ash, hickory, tulip tree (*Liriodendron tulipifera*), birch, and sassafras (*Sassafras albidum*).

Parts of Hunterdon County were settled by Europeans previous to 1700, and land unsuited for agriculture was early subject to intensified farming, with subsequent deterioration and abandonment (Schmidt, 1950). Charcoal burning, kilning, and sawmill operations were important early industries which exacted a heavy toll on the woodlands of Hunterdon County (Snell, 1881). In general, the history of the region in relation to the plant cover has been one of large scale clearing, and a heavy use of the wooded areas as a source of fuel and lumber.

Nomenclature is according to Fernald (1950).

The authors are indebted to Mr. E. B. Moore for his critical reading of the manuscript.

METHODS

The study of the vegetation of Voorhees State Park was conducted chiefly during the summer of 1954. Selected areas, believed to be illustrative of certain compositions, were traversed by belt or line transects (or both), or by means of quadrats disposed at intervals along a line. Cover values were

expressed as the percentage of the total length of the line covered by a particular species. All densities and basal areas were placed on a 1000 square meter basis, and frequencies were expressed as the percentage of the total number of quadrats, or ten meter segments of line transects, in which the species occurred or contributed to the cover. Density and basal area determinations were made, in most cases, by stem counts within a specified area for the former, and by conversion of d.b.h. readings in inches to basal area in square feet for the latter.

Dimensions of quadrats were as follows: 10 x 10 meters for arborescent species, 2 x 10 meters for saplings and shrubs, and 2 x ½ meters for seedlings and herbs. When the several size quadrats were used in any one area, the smaller were nested within the larger. Specimens of all species observed were collected for confirmation of identification and deposition in the Chrysler Herbarium of Rutgers University.

A total of 24 transects, varying in length from 30 to 200 meters, were set up for the collection of data. Locations of these transects are given in

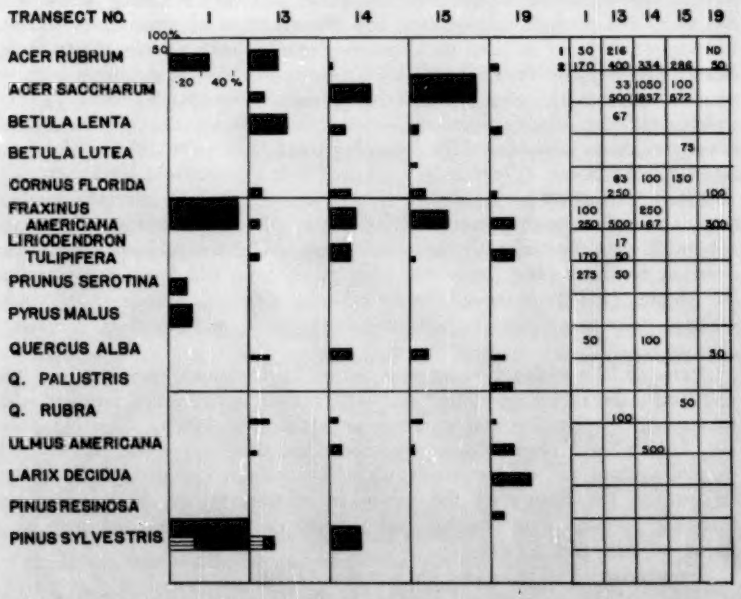

Fig. 2.—Frequency and cover values for the important tree species occurring within or adjacent to conifer plantations in the Hill Acres and Hoppock Grove areas of Voorhees State Park. Frequency of a particular species is indicated by the height of bar, and cover value by length of bar. A numerical scale is provided at the upper left. Horizontally lined portions of a bar indicate values attributable to dead standing trees. Figures at the right under transect headings give densities (No./1000 m^2) of saplings (1), and seedlings (2). No data were taken on sapling density for transect 19. The area of transect 15 contained no conifers, but is included here because it is part of a lower slope area that is used in making other comparisons in the text.

fig. 1. The information derived from certain selected transects is presented in the figures, but all data have been drawn upon in the writing of the text. The numbers found throughout the text refer to the transects as disposed in fig. 1, and hence to the conditions and composition of the plant cover in the immediate area.

RESULTS

CONIFER PLANTATIONS

In the plantation areas, deciduous species in the various size classes have become established at the periphery of the coniferous plantings, and have interpenetrated them to various degrees, the extent depending in part upon the number of casualties that have occurred among the conifers in the past (1,13, fig. 2). In certain instances, the deciduous species are of such size as to indicate that their growth had commenced at the time that the conifers were planted (white ash—*Fraxinus americana* in 1, fig. 2), or antedated them (apple—*Pyrus malus* in 1, fig. 2). A list of invaders would include most of the arborescent species occurring within the park. Those of greatest density and frequency are: white ash (1,13,14,19), tulip-tree (13,14,19), red maple (*Acer rubrum*—1,13,14,19), flowering dogwood (*Cornus florida*—13,14,19), and black cherry (*Prunus serotina*—1). Sugar maple (*Acer saccharum*—13,14) and American elm (*Ulmus americana*—13, 14,19), are important species on the lower sites. Frequency and cover data from these transects are given in fig. 2, in block diagram form, for the more important species. With the exception of 15, these transects were run entirely within a plantation (1), or through an area largely in a plantation (13,14,19). Plantation borders are often indistinct, so that except where dead conifer trees remain the boundary lines were drawn with difficulty. No plantation is free of aggressive deciduous species, at least toward the periphery, and none has as yet been completely overrun. However, there have been many casualties among the conifers since establishment, as is indicated by decaying logs and dead standing trees of various diameters.

The shrub layer associated with the conifers is generally dominated by vines, principally poison ivy (*Rhus radicans*), Virginia creeper (*Parthenocissus quinquefolia*), Japanese honeysuckle (*Lonicera japonica*), and summer grape (*Vitis aestivalis*). Gray dogwood (*Cornus racemosa*) is at times conspicuous at borders and in the larger openings, as in the red pine (*Pinus resinosa*) and Norway spruce (*Picea excelsa*) plantations near the east end of the Hill Acres road. Other shrubs of common occurrence in the deciduous woods, such as maple-leaved viburnum (*Viburnum acerifolium*), low blueberry (*Vaccinium vacillans*), and spicebush (*Lindera benzoin*), are sparingly represented in these areas. No herb species were observed to be peculiar to the conifer areas, and those species reported are generally of high frequency throughout the park (aster—*Aster divaricatus*, white snakeroot—*Eupatorium rugosum*, cinquefoil—*Potentilla canadensis*, and violet—*Viola* spp.). They can be found at the borders, and, in association with the deciduous invaders, penetrate into the plantation.

With regard to natural regeneration of the conifers, observations throughout the park indicate that scotch pine (*Pinus sylvestris*) becomes established

in fair abundance in some of the fields and openings close to a seed source. Successful reproduction of the remaining species (white pine—*Pinus strobus*, European larch—*Larix decidua*, red pine, and Norway spruce) occurs, but is widely scattered and not prominent.

In the heart of a plantation, the growth is very dense, all lower limbs are shaded out, and the floor consists of a relatively sterile layer of undecayed needles. Occasionally toward the periphery, these areas are penetrated by poison ivy, and sometimes by Virginia creeper. These scattered stems form the only ground cover. Where the soil layer is exposed, several mosses (chiefly *Polytrichum commune* and *Leucobryum glaucum*) may be found.

OAK WOODS

The more important tree species occupying the ground on the upper, steeper slopes are chestnut oak, red oak, sweet birch and red maple. Reproduction of the dominant species, chestnut oak, is chiefly of sprout origin. Red maple is abundant in the lower size classes, and appears to be the common species of openings, along with the sprouts of chestnut oak, and to a lesser extent, with the young saplings of sweet birch. The soil layer is at its thinnest on these upper slope areas, many boulders lying exposed and covered with bryophytes or crustose and foliose lichens. A generally low average tree volume when compared to lower slope areas is indicated by basal area measurements.

The shrub layer on the upper slope is of moderate density, with a good representation of maple-leaved viburnum, and such ericads as low blueberry, pinxter flower (*Rhododendron nudiflorum*), and black huckleberry (*Gaylussacia baccata*). As on all of the higher ground, wild sarsaparilla (*Aralia nudicaulis*) is particularly prominent in the herb layer, along with aster, sessile-leaved bellwort (*Uvularia sessilifolia*), whorled loosestrife (*Lysimachia quadrifolia*), and violet (*Viola papilionacea*).

Tree cover on a more gentle slope in the same section of the park, and on nearly level ground, differs to the extent that the so-called "better oaks" (red oak, white oak—*Quercus alba*) are more evident. Two other oak species well represented on the higher parts of the park in general are black oak (*Quercus velutina*) and scarlet oak (*Quercus coccinea*).

The land behind the old orchard field (3) slopes rather steeply to the northwest and west, and more gently to the northeast. The drainage in this area is into Willoughby Brook by way of several anastomosing streams in the lowest ground of the central tract (central stream, fig. 1). Except for a few naturally produced openings, the land here is occupied chiefly by several species of oak, red maple and sweet birch (8,10,11, fig. 3). Improved site quality, as compared to the upper slope woods, is reflected in a tendency toward a greater frequency and percentage cover of such species as red oak, tulip tree and white ash. Chestnut oak continues to be of some importance below midslope, although growth form is poor, and dead standing trees are frequently encountered. A late successional stage is illustrated by 10. This area was undoubtedly formerly used as a pasture, but its use was discontinued sufficiently long ago to allow for the development of 4"-5" d.b.h. specimens of large-toothed aspen (*Populus grandidentata*) and gray birch (*Betula*

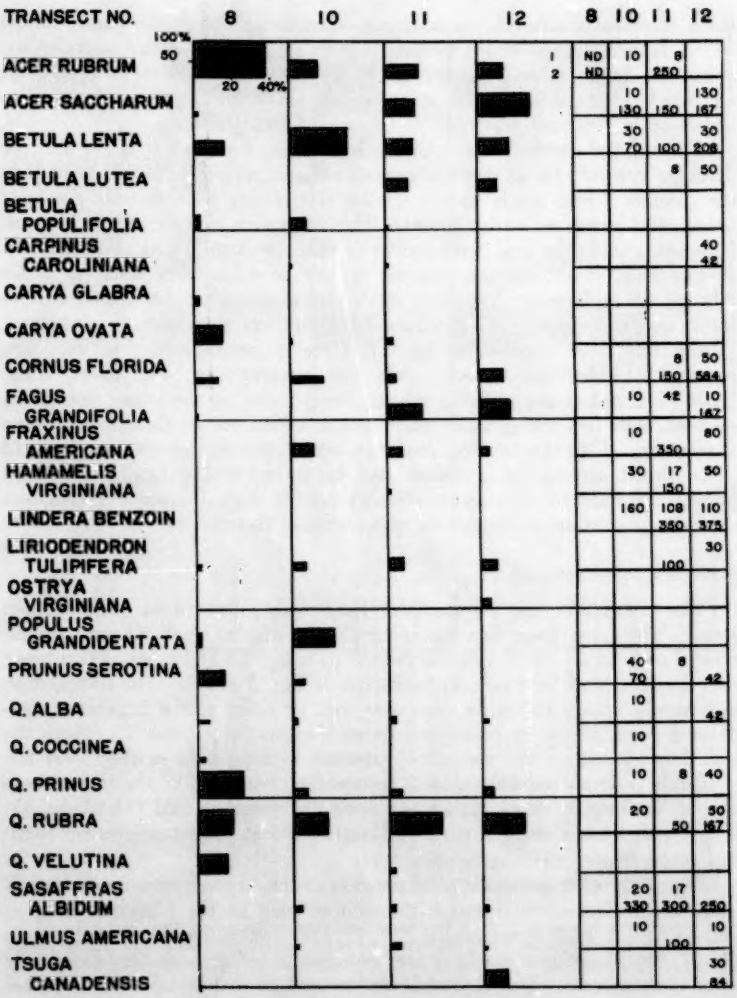

Fig. 3.—Frequency and cover data from four transects run through the woodland behind the old orchard field. Areas represented are: top of slope (8), mid-slope (10), lower slope (11), and valley bottom (12). Presentation of data as in fig. 2.

populifolia) with transgressives of red maple and sweet birch, and to a lesser extent red oak, tulip tree, and white ash.

Thirteen species of shrubs were found on this slope, ranging from those of common occurrence on the upper slopes as mentioned above, to

those of spare distribution or scattered occurrence through the park. Those in the latter category would include pagoda dogwood (*Cornus alternifolia*), American hazel (*Corylus americana*), deerberry (*Vaccinium stamineum*), and black highbush-berry (*V. atrococcum*). Wild sarsaparilla continues to dominate in the herb layer.

Toward the northeast from the orchard field, the slope is slight and the drainage less definite, so that the ground remains noticeably moist throughout the summer. Red maple in the smaller size classes predominates here and forms solid stands of limited extent. Thicket growth of spicebush at intervals is conspicuous. The best development of ferns, in density and variety, occurs in this area. Herb species common to wet or mesic sites, such as skunk cabbage (*Symplocarpus foetidus*), small Jack-in-the-pulpit (*Arisaema triphyllum*), and May-apple (*Podophyllum peltatum*) are abundant.

On the lower slopes (11, fig. 3), there is interdigitating of the components of the oak woods with the elements of the lower mesic areas. Red oak is the unifying species, being found in the larger size classes on both high and low ground. The tree reproduction on these lower slopes is plentiful. Oak sprouts and seedlings are chiefly of chestnut oak and red oak. Small saplings of sassafras and black cherry are locally abundant. Sprouts of chestnut (*Castanea dentata*) are of high frequency throughout the slope, and attest to the former importance of this species.

NORTHERN HARDWOODS

The distribution of the northern hardwoods is restricted to the lower areas. The most important species are sugar maple, beech (*Fagus grandifolia*), and yellow birch (*Betula lutea*) (15, fig. 2; 11,12, fig. 3). These data are presented for frequency and cover in figs. 2 and 3. The composition is generally incomplete in any one area, one or more of the important components being absent or poorly represented, except in 11 and 12, where the best development of this community appears to have been reached thus far.

Beech is firmly established and apparently expanding in the downstream area of Willoughby Brook, as well as along the central stream (11,12, fig. 3). It is on this lower slope toward Willoughby Brook that transgressive beech and sugar maple may best be seen.

Regarding other components of the northern hardwood community, yellow birch is found scattered through the western part of the Hoppock area, as well as by the Hill Acres bridge (15, fig. 2), and along the central stream (11,12, fig. 3). Sugar maple is also established and reproducing abundantly in all of these areas. It also extends further upslope than some of its associates (8, fig. 3), and clearly exceeds them in frequency and density, chiefly in the smaller size classes. Tulip tree and white ash, although particularly characteristic of the mesic sites, are also successful on high ground. Red oak may be found throughout the wooded area. Hornbeam (*Carpinus caroliniana*) and hop hornbeam (*Ostrya virginiana*) are locally important in the more mesic sites. The section enclosed by the main park drive contains a good development of American elm and pin oak (*Quercus palustris*), the latter being of limited occurrence elsewhere in the park.

The shrub layer of the mesic woods is rather uniform. Spice bush is of

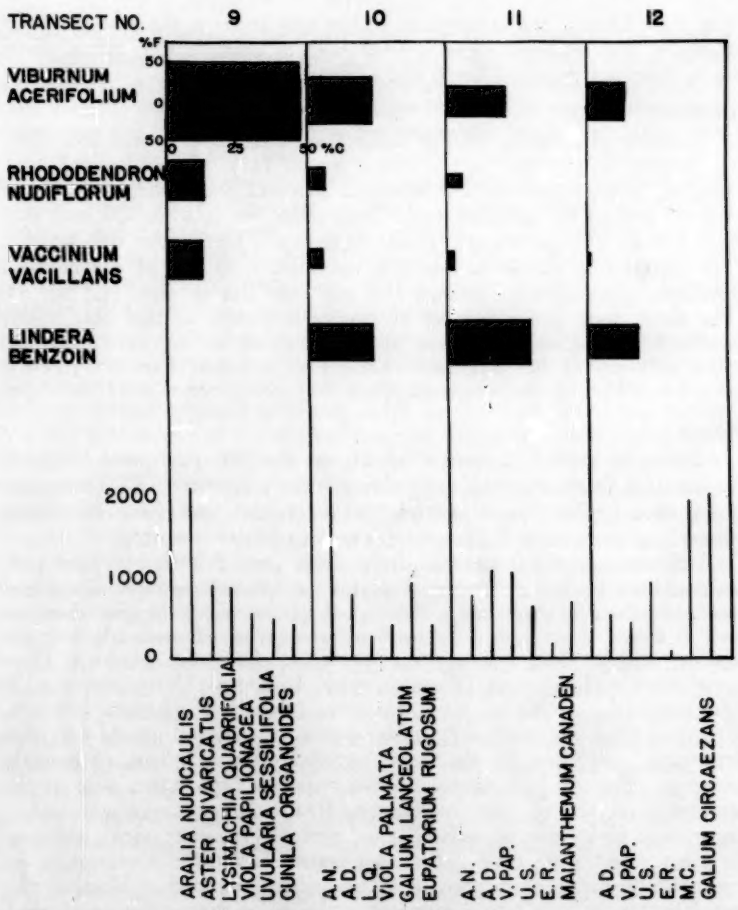

Fig. 4.—An illustration of frequency and cover values for several of the more important shrub species, and density values per 1000 sq m for the principal herbaceous species. Data from the series of downslope transects north of the old orchard field. Names of herbaceous species are abbreviated after the first time they appear in order to emphasize the first appearance of each.

greatest importance, and on the lower ground reaches its best development. Scattered specimens may be found for a considerable distance upslope. In contrast, the ericads and maple-leaved viburnum, while most important on the upper slopes, decrease toward the mesic lower slopes where the northern hardwood community predominates (fig. 4).

In the herb layer, the heavy cover of wild sarsaparilla of the upper slopes gives way to a mixture of species in the northern hardwood community

(fig. 4). Density and composition of the herb layer on the mid and lower slopes is not uniform. Tree reproduction is chiefly sugar maple, sweet birch, flowering dogwood, beech and white ash.

HEMLOCK

A stand of hemlock (*Tsuga canadensis*) occupies a limited area along the extreme western part of the central stream (12). There is some intermingling of the coniferous and deciduous elements, and saplings of hemlock may be seen as transgressives under large specimens of white oak and shag bark hickory (*Carya ovata*). Here hemlock and beech grow side by side. The composition of the surrounding woodland is largely of the northern hardwood type, although remnants of oak may also be seen (12, fig. 3). The shrub layer under hemlock is sharply restricted, so that only widely scattered maple-leaved viburnum and spice bush are to be found, and these only toward the periphery. Little but Christmas fern (*Polystichum acrostichoides*) and beech-drops (*Epifagus virginiana*) occur in the herb layer.

FIELDS

The open ground is confined mainly to the Hill Acres and Hoppock Grove areas, the central tract being almost entirely in woodland. These open areas were formerly in cultivation, or in pasture, and some have been allowed to revert since the property came into public ownership.

Differences in the treatment of the fields located in each of the park sections have resulted in the presence of somewhat different species aggregations. In the Hill Acres area, the strip of ground along the park drive, as well as several small fields adjacent to it, are regularly mowed. As a consequence, only low-lying and rosette plants (cinquefoil, wild strawberry (*Fragaria virginiana*), plantain (*Plantago* spp.), hawkweed (*Hieracium* spp.)), and perennials capable of quick recovery, (chicory (*Cichorium intybus*), goldenrod (*Solidago nemoralis*)), were prominent. Several grasses were also important contributors to the cover: orchard grass (*Dactylis glomerata*), bluegrass (*Poa* spp.), bentgrass (*Agrostis* spp.). Data taken early in the summer from one of these roadside fields (2) before mowing showed a particularly high cover of orchard grass, probably an effect of its wide use as a hay crop. King devil (*Hieracium pratense*), equally prominent, is an aggressive plant in most open areas throughout the park. Most of the remaining species were typical members of the weedy flora—common ragweed (*Ambrosia artemisiifolia*), soft chess (*Bromus mollis*), Kentucky bluegrass (*Poa pratensis*), and dandelion (*Taraxicum officinale*).

The peach trees were removed from the old orchard field (3) early in 1953, with the expectation of establishing a suitable grassy area here. However, foxtail grass (*Setaria glauca*) had become established previous to tree removal, and despite several mowings during that year, and plowing of the field in the spring of 1954 followed by seeding with a standard grass mixture, this grass has persisted. Such a situation has been noted elsewhere by Beckwith (1954), who attributes the success of foxtail as a colonizer of cultivated ground to the possession of a heavy seed, capable of long periods of dormancy —factors which lead to concentrations in restricted areas and to resistance to temporary unfavorable environmental conditions. The grass is weakly com-

petitive, but the plowing of the orchard field has had the effect of destroying the plant cover and creating the seed bed conditions best suited to its development. A detailed study of the herb cover of this field was made in June, when the new growth of foxtail had just begun. The species list obtained at that time was quite varied, most of the components being in the early vegetative stage. By mid-July, foxtail had overgrown all else, except for some large patches of smooth crabgrass (*Digitaria ischaemum*), and scattered specimens of yellow rocket (*Barbarea vulgaris*), common mullein (*Verbascum thapsus*), and Canada thistle (*Cirsium arvense*). The original species list made in June had totaled 34, of which milfoil (*Achillea millefolium*), orchard grass, common ragweed, butter and eggs (*Linaria vulgaris*), and Canada bluegrass (*Poa compressa*) were most prominent.

The power line clearing (fig. 1) is visited at intervals by workmen who, in the process of keeping the line open, destroy or damage the ground cover over extensive areas by cutting and by the application of herbicides. Use of the latter method appeared to be responsible for the death of all angiosperms in a 100 yard length of the clearing south of the orchard field during June. By late summer, only Virginia creeper and hairy-vetch (*Vicia villosa*) had reappeared. The plant cover of this clearing may be described as a mixed perennial herb type (Graham, 1953). There is scattered sapling development of species characteristic as old field pioneer trees, black cherry and gray birch being most frequent. A cover of orchard grass and tall oat grass (*Arrenatherum elatius*) is particularly high in the herb layer in that part of the line near the orchard field (4). Southeastward, a large colony of the bracken fern (*Pteridium aquilinum*) is invading this open area.

To the southwest of the picnic area in Hoppock Grove, there may be found what was one large field. The old fence rows, composed of boulders and rocks previously removed from the ground, may still be seen. Outward movement of the woody species has proceeded from the peripheral woods to the east, west, and south, and from fence rows which once separated the portions of the field. The total effect has been to reduce the southwest portion to a number of relatively small openings. The section of the field investigated in detail was one of the larger ones, located adjacent to the picnic area (17).

The herb, shrub, and sapling composition agree in general with the average 25-40 year old fields found by Bard (1952) in the study of old fields in the Piedmont, although differences were evident, chiefly in the relative roles of hawthorn (*Crataegus pruinosa*) and red cedar (*Juniperus virginiana*) as pioneer species. In this field, gray dogwood plays a leading part in the invasion, and hawthorn is nearly as important. Red cedar is distinctly minor, the occurrence of this species being so scattered that no specimen fell within a quadrat or under a line. Among trees established in sapling size, black cherry was the most important. Cover values for the more important woody species, in percent of total line transect length, were as follows: gray dogwood (22.4), hawthorn (8.1), black cherry (6.1), sassafras (4.6), American elm (4.5), and red maple (2.9). Poison ivy (18.3), and Virginia creeper (9.2) move out early along with the shrub cover and attain a high density.

Throughout large portions of the field there is considerable sod develop-

ment: redtop (*Agrostis alba*), Kentucky bluegrass, and Canada bluegrass cover extensive patches of ground, and poverty-grass (*Danthonia spicata*) is equally prominent. Tufts of little bluestem (*Andropogon scoparius*) and Indian grass (*Sorghastrum nutans*) become evident, but not dominant, later in the season. The northeast side of the field is bordered by a young woods of sweet birch, with little undergrowth. In this young woods, the elsewhere prevalent species, such as gray dogwood, poison ivy, and Virginia creeper, are absent or widely scattered. The ground cover here is mainly in bramble (*Rubus flagellaris*), wild strawberry, cinquefoil, and goldenrod (*Solidago juncea*). The trees appear to have invaded the margin of the field before there was any appreciable establishment of shrubs.

DISCUSSION

The impression created by the study of the vegetation of Voorhees State Park is one of instability, but with some suggestion of the pattern that might result from the attainment of a condition of relative stability. Even under present conditions, there is a prevalence of the northern hardwood type and hemlock on the lower ground, while the upper slopes and ridges are occupied to a considerable extent by oak. This may be observed by a comparison of tree composition on high and low ground as illustrated by means of a series of phytographs (fig. 5). The successive downslope transects in fig. 2 (13,14,15) and in fig. 3 (8,10,11,12), reveal a similar disposition. The present importance of red maple and sweet birch may also be noted.

Reasonably similar patterns have been indicated elsewhere in the same physiographic region. Although the Voorhees area is not sufficiently large nor varied topographically to accommodate the number of forest communities delimited by Niering (1953) in High Point State Park, a correspondence is evident in several instances—his chestnut oak community with the tree composition of the area traversed by transect 7, his mixed oak-hardwood with 18, and his northern hardwood without hemlock with 11 (fig. 3). That the beginnings of a hemlock-hardwood community also exist is indicated by the data from transect 12 (fig. 3), a type which would develop further with the continued expansion of hemlock. The nearest approach to a swamp hardwood community might be referred to the young growth of red maple, with some sweet birch and yellow birch upstream in the central tract.

Distribution of the tree species in the Black Rock Forest of the Hudson Highlands (Raup, 1938) also conforms to this pattern. White oak and pignut hickory (*Carya glabra*) are predominant on the north and east sides of the hilltops, chestnut oak and red oak on the upper slopes, and hemlock, tulip tree, white ash, sugar maple, red maple, sweet birch, and beech on the lower slopes and valleys. These last mentioned species are recognized as constituting hemlock-hardwood, mixed hardwood, and northern hardwood communities, depending upon the way that they aggregate in any particular area.

On the slopes of nearby Cushetunk Mountain, the results of Cantlon's study (1953), based on the total basal area of all trees over 1" d.b.h. occurring within the quadrats, indicate that white oak and black oak were mainly confined to the drier south-facing slope, and that chestnut oak and

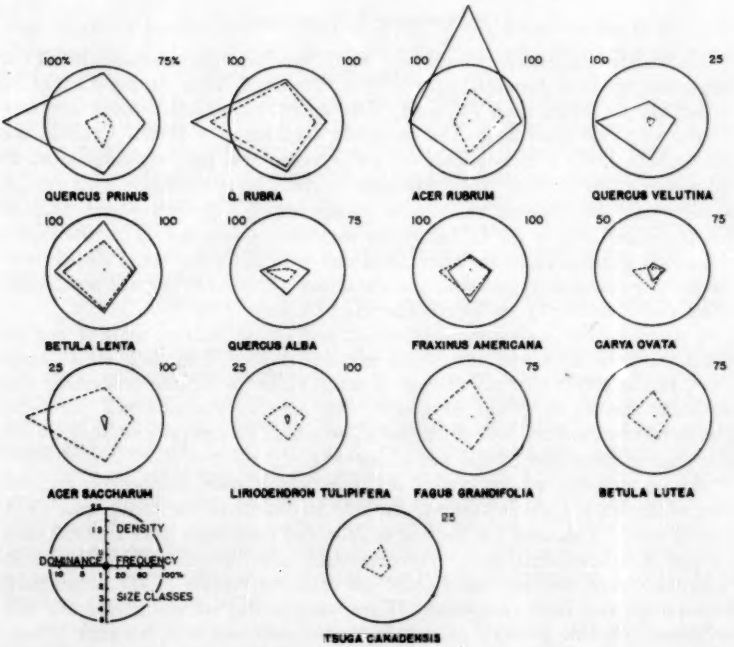

Fig. 5.—A series of phytographs depicting the importance of a number of tree species on high (solid line), and low (dotted line) ground with respect to four values: density (number of individuals over 1″ d.b.h. per 1000 sq m), frequency (percentage of quadrats in which the species occurred), number of size classes represented by individuals of a species (seedlings, saplings, and 1-3.9″, 4-9.9″, and 10″ + classes), and dominance (percent basal area of a species). The 700 foot contour was arbitrarily set as the dividing line. The phytographs are a modification of those described by Lutz (1930). The scale at the lower left shows that the maximum values of density and dominance do not coincide with the length of the radius, but are scaled so as to obtain polygons of convenient size for comparison purposes. The data represent averages from four transects in each situation, and the figures to the upper right and left of each phytograph represent the constancy of the species among the stands sampled on the high and low ground respectively. For example, *Quercus prinus* occurred in the quadrats in all four stands sampled (100% as indicated at the upper left) on the uplands, but in only three of the four (75% as indicated at the upper right) in the lowlands. There were 22 individuals of this species (density) per 1000 sq m on the uplands compared with 4 per 1000 sq m on the lowland. It had a frequency of 77% on the uplands but only 17% on the lower ground. It occurred in all but one size class on high ground, but in only two size classes on the low ground. Its dominance as indicated by basal area was 23% on the high ground, but only 4% on the low ground.

red oak were also well represented on this slope although showing greater basal area values on the north-facing slope. Again, such species as sweet birch, tulip tree, white ash, red maple, and beech had their best representation on the more mesic north-facing slope.

SECONDARY SUCCESSION

Secondary succession within the park involves the reestablishment of vegetation on land formerly cultivated or pastured. Due to the absence of cultivation for more than 25 years, the earliest successional stages are now absent, with one exception. The persistent recurrence of foxtail grass in the old orchard field, a consequence of the mowing and plowing subsequent to the removal of the fruit trees, has been referred to previously. This species is an annual of common occurrence throughout this general region and, in this particular case, is the initiator of a secondary succession. The dominance of various annuals on fields abandoned one year has been noted elsewhere—particularly common ragweed in the Piedmont (Bard, 1952), and horse-weed (*Erigeron canadensis*) in North Carolina (Keever, 1950).

A perennial herbaceous stage is represented on the narrow strip of ground along the park roadways and small adjacent fields. This is a semi-natural cover, to the extent that no attempt is made either to include or exclude any particular species or group of species, but only to maintain the particular growth form considered best suited for these areas. Its composition is undoubtedly greatly influenced by the annual mowing.

As an example of fields and openings which now support shrubs and trees which are not shade tolerant, the field southwest of the picnic area (17) may be cited. This land was farmed or pastured some time prior to 1929, and has not been disturbed since. Another field, the former CCC campsite in Hoppock Grove, was not freed from use until the middle 1930's, when park development had been completed. Water supply and storage shacks are still maintained on this ground, so that moderate disturbance is frequent. Here, only gray birch and Scotch pine are prominent woody invaders, and observations indicate that cover values for woody species are far less than in the previously mentioned field southwest of the picnic area (17).

A large part of the eastern section of the Hill Acres tract had been in orchards while the land was a private estate. When the conifer plantations were established in 1932-33, there was some interplanting of the conifers among the remaining fruit trees. A number of these trees (peach—*Prunus persica*, apple, and pear—*Pyrus communis*) still persist, surrounded by conifer and deciduous elements.

A late successional stage, involving large-toothed aspen and gray birch, is represented in the mid-slope area behind the old orchard field in Hill Acres (10, fig. 3). This slope probably had been used only for pasturage, and the abandonment of this practice gave the succession its start here.

The plantations also represent a successional stage because of the inability of the conifers to compete successfully with the deciduous species.

Several species, often regular components of the mature woodland, may be observed to initiate directly the secondary succession in woodland openings and small clearings, chiefly in the Hoppock Grove tract. Immature, even-age stands of red maple or sweet birch (or a mixture of both) may frequently be seen here and in the southeast portion of the central tract. Red maple is occasionally present in the overstory, and sweet birch is frequently seen in this position in mature portions of the woodlands, chiefly on the upper slopes. Both are of high frequency and density throughout the wooded area. How-

ever, wherever beech-maple on the one hand, or oak forest on the other (with the exception of chestnut oak) have been rather long established, the red maple and sweet birch are only minor constituents.

Yellow birch is an important species in the lower areas, and many pole-size logs may be seen on the forest floor. Yellow birch is a normal component of the northern hardwoods. It may be relatively unsuccessful here at the margin of its range—of successional significance, but not vigorous. Pin oak and American elm are locally important as transgressives, chiefly in the conifer plantations in the Hoppock Grove area. Certain common large shrubs, such as witch-hazel (*Hamamelis virginiana*) and spicebush, show little tendency to colonize open areas.

Of first importance in a successional study here is the relationship among oak, beech-maple, and hemlock. At the present time, mature specimens of oak (white, chestnut, red, and black oak) may be found throughout the park, the white and red oak predominating in the larger size classes on the undisturbed lower ground, except in those areas where a mature northern hardwood community is present. Density of white oak is generally low, much of the cover and basal area being attributable to mature specimens. One of the two specimens of white oak with the greatest d.b.h. (24″) is located at streamside in the central area, and is surrounded by saplings of hemlock. Large size shag bark hickory (*Carya ovata*) are present here also. There is a temptation to refer to these veteran oaks and hickories as relicts of the former forest community which once was dominant where now the northern hardwood and hemlock communities occur.

As previously noted, the area occupied by hemlock within the park is sharply restricted, and evidence that this species is expanding its territory is in the form of saplings and young trees that are to be found at the boundaries of the more concentrated growth. Beech is somewhat less restricted, and may extend for a limited distance upslope, as is the case toward the western portion of Willoughby Brook. Sprouting from the roots affords this species a dependable means of reproduction, and this feature, combined with a high shade tolerance, guarantees its persistence in those areas where it becomes established. Another important northern hardwood component, sugar maple, extends farthest upslope, outliers being found on the highest ground. Saplings of this species are frequently seen among pioneers of previously open ground, as on the lower slope by the Hill Acres Bridge (14), where the sugar maple saplings have overtopped dead and dying specimens of hawthorn and smooth sumac (*Rhus glabra*). Although much of the growth of sugar maple is at present in the younger size classes, there is no reason to believe that it will not progress to maturity, granting continued freedom from disturbance. Regarding this species as a colonizer, it would appear that such factors as presence of a protective cover, and reasonable freedom from root competition, influence its successful establishment, since it is seldom found in open fields where the sod forming grasses predominate, but rather within the shade of the woodland where the herbaceous growth is generally sparse.

While oak species continue to become established throughout the park to a considerable extent, the reproduction is not as aggressive as that of other species, suggesting that the oak will more and more share dominance. On the

lower ground, as we have already seen, there is evidence that the oak woods is giving way before an expanding northern hardwood community. In these lower areas, such species as beech and sugar maple enjoy certain advantages of a physiological nature, such as shade tolerance, which makes succession in their direction probable.

PRACTICAL CONSIDERATIONS

The establishment of plantings within the park must have had landscaping as its objective. Certainly the blocks of conifers here and there through the park do add to the diversity within the area. Other possibilities seem to be ruled out. Timber production, for example, is not a function of parks. Erosion control would not enter since, as we have seen, in this humid region the natural succession covers the ground with protective vegetation rather rapidly. To some extent the conifers may serve as wildlife cover, particularly in the younger stages, but as a general source of wildlife food they are inferior to the various intermediate stages of natural succession.

It is unfortunate that the hemlock, native and successful in the park, was not more widely used in the plantings. Young hemlock grow even in the shade of the deciduous trees. Had it been used instead of the exotic suppressed Norway spruce in the woods around the picnic area, the desired understory of evergreens would have been attained. Had it been used in place of some of the exotic species in the plantations, much more successful and permanent conifer stands could have been attained, and in general some of them would have been more attractive. However, the heavy mortality of hemlock in forestry plantings makes it generally impractical to plant (E. B. Moore in correspondence).

Maintenance of the earlier successional stages for purposes of landscaping and provision of high wildlife food and cover may be handled in several ways. The regular mowing of the roadsides and playfields is one method now in use. This is necessary where a lawn-like effect is desired, but it is relatively expensive. Selective use of herbicides can make possible the attainment of a dominance of shrubs and grasses into which invasion by other plants is slow (Egler, 1948). In the maintenance of telephone, power line, and roadside rights of way, it is possible to develop relatively permanent shrub types by the removal of unwanted species by selective herbicide basal spraying. Those to be removed would include trees and probably other species such as poison ivy. It is basically a matter of assisting the desired shrub species to gain complete dominance, after which they appear able to hold it for a relatively long time (Egler, 1949, 1950, 1954). Such a procedure for the development of relatively stable low-growing types of vegetation is far less expensive in the long run, much more productive of wild life cover and food, and preferable from the landscaping point of view to the traditional method of allowing young thickets of trees to grow up and then to slash them down with the axe from time to time. On the other hand, indiscriminate broadcast spraying that is now coming into common usage is not only productive of unstable plant communities that need repeated treatment; it is destructive of wildlife values, and from the landscaping point of view exceedingly undesirable.

Such selective vegetation control as is recommended here should perhaps

be applied to the old fields in intermediate stages of succession to keep them in much the same condition as they are now, because they represent especially desirable types to maintain for variety in the park. They serve not only to produce diversity in vegetation but help to maintain a high population of native animals.

SUMMARY

Voorhees State Park has had a long history of disturbance, and it is only within the past two decades that any measure of freedom has been provided for the reestablishment of a natural vegetation. The general status of the vegetation is one of instability at present.

Two natural forest communities are important within the park. Oak is the most extensive, occurring throughout the wooded area. It is most important on the higher ground. With the oaks there are two associates—red maple and sweet birch. The second natural forest community, the northern hardwood, is found on the lower slopes, and at one place the hemlock achieves dominance.

The various stages of secondary succession are found within the park. Gray dogwood and hawthorn are most important among the earlier established woody species. Black cherry, sassafras, white ash, red maple, large-toothed aspen and gray birch are tree species in the succession, and are primarily responsible for the aspect in the later stages.

Many of the conifer plantations, planted about 1932, are poorly established, and are being invaded by native species.

It is recommended 1) that any future plantation preferably consist of successful native species, and 2) that systematic vegetation control by careful selective herbicide treatment be instituted along rights of way and in old fields, in order to retain or develop highest wildlife and landscape values. Broadcast herbicide treatment should be discouraged as it is a highly undesirable method of vegetation control.

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Regional Variation Patterns in the Stemless White Violets[1]

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In this and a paper to follow studies on the stemless[2] white violets, initiated by the author in 1948, will be summarized. This research has resulted in several publications which are cited individually below. In the course of the research, many botanists have offered advice and encouragement to the author. Appreciation is especially due Dr. Gerald B. Ownbey of the University of Minnesota and Dr. William S. Cooper of Boulder, Colorado, for their assistance in early stages of the work. Dr. Cooper supplied much of the information regarding the history of "Orange Island", discussed under *Viola lanceolata*. The interest shown and advice given during the investigations by Dr. Ernst Mayr of Harvard University and Dr. Edgar Anderson of the Missouri Botanical Garden have been very helpful.

Two studies used as guides in defining the aims of the present research were those of Woodson (1947) on *Asclepias tuberosa* and of Cain and Dansereau (1952) on the stemmed yellow violets of eastern North America. Certain of the methods used were borrowed from these studies. The object of the present paper is to provide a relatively exhaustive analysis of morphological variation from herbarium specimens and population samples and then to use these data in a consideration of the present evolutionary status of the group. This type of study is frequently found in recent literature, but, since Brainerd's investigations (summarized in his work on hybrid violets, 1924), little research of this nature has been done in *Viola*. Most of the studies in *Viola*, such as those of Valentine (1941, 1950) and Clausen (1924, 1926, 1930, 1931), have been concerned with cytological details and the relationships of chromosome number to morphological appearance and geographic range.

The taxonomy of the stemless white violets is treated in a separate paper (Russell, 1955). The six species there recognized belong to the Group *Stolonosae* of the Subsection *Plagiostigma*, Section *Nominium*, of *Viola*. Four of the species, *V. lanceolata*, *V. primulifolia*, *V. macloskeyi*, and *V. renifolia*, have the chromosome number of $2n = 24$ and compose the "subgroup" *Primulifoliae*, and the remaining two, *V. blanda* and *V. incognita*, with the chromosome number $2n = 44$ or 48 (Clausen, 1929), are placed in the "subgroup *Blandae* (Gershoy, 1934; Bamford and Gershoy, 1930). All six of these violets are quite small, seldom exceeding a few inches in height. They have small, petiolate leaves arising from short, compact stems which

[1] Part of the material in this paper was taken from a Ph.D. dissertation completed in the Department of Botany, University of Minnesota, Minneapolis.

[2] The "stemless" or "acaulescent" violets actually possess well-developed stems, but these are almost completely underground. The "stemmed" violets, on the other hand, have erect, leafy, aerial stems.

remain at or below the surface of the soil. All but one (*V. renifolia*) have long, vegetative stolons. In the early spring (and sometimes in late autumn) they produce small, white, petaliferous flowers, the petals bearing conspicuous purple veins. Throughout the summer cleistogamous flowers are abundantly produced.

The stemless white violets occur in small local populations, a consequence of the usual size of the habitats to which they are adapted. Under favorable circumstances they may develop dense, slightly matted stands. They are generally found in cool, wet locations, varying from open sphagnum bogs to coastal swamps and rich deciduous forests.

METHODS OF STUDY

The approximately 5,000 herbarium specimens examined were borrowed from twenty large herbaria, to which appreciation has been expressed in another paper (Russell, 1955). Twelve characters were measured or observed on the specimens, and scoring indices were set up for each character. Measurements involved in the present analysis are briefly defined below. Some of them have been discussed at greater length elsewhere (Russell, 1952; Russell and Cooperrider, 1955).

Lamina length.—The shortest length of the leaf blade, measured along the midrib and expressed directly in millimeters.

Lamina breadth.—This was measured at right angles to the midrib at the broadest part of the limina, and was also expressed in millimeters.

Leaf pubescence.—Pubescence of four areas was considered. These areas were:

Upper surface of lamina.—Scoring was as follows: 0 if entirely glabrous; 1 if a few hairs were found on the major veins; 2 if both the veins and some inter-vein surfaces were hairy; and 3 if the whole surface was uniformly pubescent.

Lower surface of lamina.—Scored as the upper surface.

Leaf margin.—Scored as either glabrous (0), or pubescent along half or more of the leaf perimeter (1).

Petiole.—Scored as 0 if glabrous or with 1-4 scattered hairs, or 1 if more pubescent.

The above characters were among those chosen for study after an extended examination of both herbarium specimens and the literature had indicated that they are not only significant taxonomically but relatively easy to deal with. Only mature specimens were measured. Greenhouse growth studies had previously been made, so that leaf maturity was recognized. As in most plants, leaf shape in violets does not cease changing until the leaves reach a certain age.

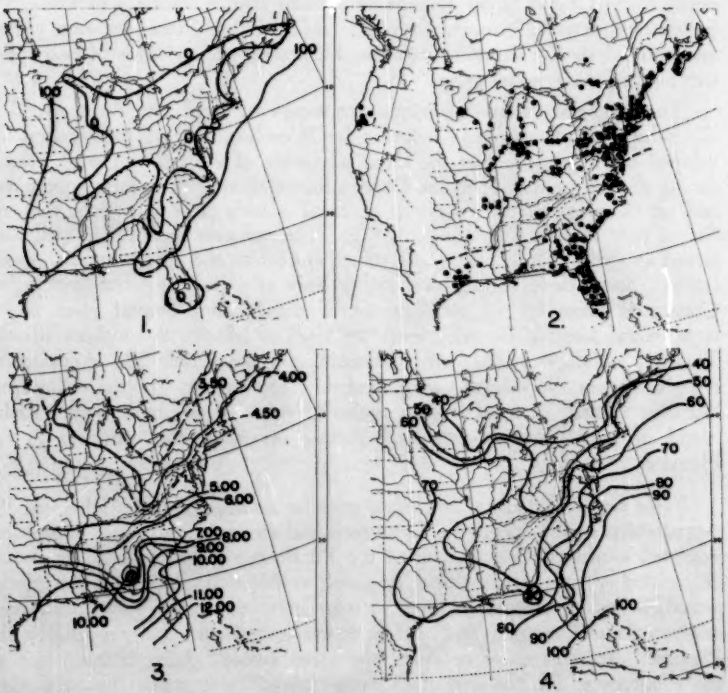
The maps that follow were prepared in the following manner. First, a large map of North America was divided into squares 100 miles on a side. The measurements for each species of violet were then located in the areas where they had been collected. When this had been completed, means were obtained for each character in each area where five or more plants had been obtained. These means were then mapped for each character, and phenocontours (isorhythms) were drawn, if possible. It is obvious that with the use in some areas of as few as five specimens and in others of as many as fifty the statistical validity of the means must vary greatly. However, a large number of areas were available, and the contour lines were usually drawn without much difficulty. The presence of definite geographical char-

acter gradients indicates that, in spite of the roughness of these methods, they do yield positive results.

VIOLA LANCEOLATA L.

This violet is represented by three subspecies, which are both morphologically and regionally well defined. These are subsp. *occidentalis* (Gray) N. H. Russell in southwestern Oregon and northwestern California, subsp. *lanceolata* in central and northeastern United States, and subsp. *vittata* (Greene) N. H. Russell along the coastal plain in southeastern and southern United States. These latter two subspecies have not been indicated separately on the map (fig. 2), but the dotted line approximately separates their range. Though large, mature plants of the two subspecies are easily separated, small, immature plants are often very difficult to distinguish.

The subspecies of *V. lanceolata* may be distinguished most easily by the



Figs. 1-4.—1. Total pubescence values for the eastern subspecies of *V. lanceolata*. A reading of 0 indicates the leaf was completely glabrous; a reading of 100 that it was slightly pubescent. 2. Natural distribution of *V. lanceolata*. Each dot indicates a herbarium specimen examined. The dots in Oregon and northern California are for specimens of *V. lanceolata* subsp. *occidentalis*. 3. Lamina length/breadth ratios for the eastern subspecies of *V. lanceolata*. 4. Lamina length measurements in millimeters for the eastern subspecies of *V. lanceolata*.

shape of the lamina and, in the two eastern subspecies, by the amount of leaf pubescence. Leaf shape varies from ovate in the isolated subsp. *occidentalis*, through lanceolate in subsp. *lanceolata*, to linear or linear-lanceolate in subsp. *vittata*. The index derived by dividing the length of the lamina by its breadth has been used to indicate lamina shape. In fig. 3 are shown the results of plotting lamina length/breadth ratios and then constructing phenocontours. There is a very broad north-south cline, interrupted to some extent in the eastern mountains and in southwestern Georgia. There is obviously no sharp division between the two subspecies, though, for taxonomic purposes, a ratio of about 5.50 may be used to separate them.

Lamina length (fig. 4) also increases regularly from north to south, again with plants with "northern" characteristics extending far southward along the mountains. In fig. 1, a numerical value indicating the total pubescence of the leaf has been plotted. Glabrous plants (value 0) are most abundant in northeastern United States (except for a small area in southern Florida), and pubescence increases outward from this area. Other characters were plotted and showed similar variation patterns, illustrating the presence of two rather well-marked eastern subspecies.

These general variation patterns are somewhat similar to those found in the subspecies of *Asclepias tuberosa* by Woodson (1947). Woodson developed the hypothesis that the three subspecies of *A. tuberosa* were isolated during the early Cenozoic in the Ozarks, the southern Appalachian mountains, and on "Orange Island", a group of small islands once located in the area that is now Florida (Woodson, 1947). The last two areas might well have served as refugia for *V. lanceolata* subsp. *lanceolata* and subsp. *vittata*, respectively. These three regions presumably were effectively isolated first in late Cretaceous times by the submergence of the Atlantic coastal plain and a large inland sea that extended from the Gulf of Mexico to southern Illinois. This sea withdrew in the early Cenozoic, and the Ozark and Appalachian refugia (sensu Woodson) were probably reconnected in the Oligocene. "Orange Island" changed from a group of small islands to a single, sizable island in early Cenozoic time and became united to the continent in the Pliocene.

Viola lanceolata subsp. *lanceolata* may be assumed to have inhabited the Appalachian region during the Cretaceous and the early Tertiary. It probably migrated southward during each of the Pleistocene glaciations and reinvaded deglaciated territory from New England to Minnesota in each interglacial period, including postglacial time. *Viola lanceolata* subsp. *vittata* may have originated on "Orange Island" before it was united with the mainland in the Pliocene. It must have occupied the inner coastal plain during much of the Pleistocene, for the site of "Orange Island" was repeatedly submerged during interglacial stages.

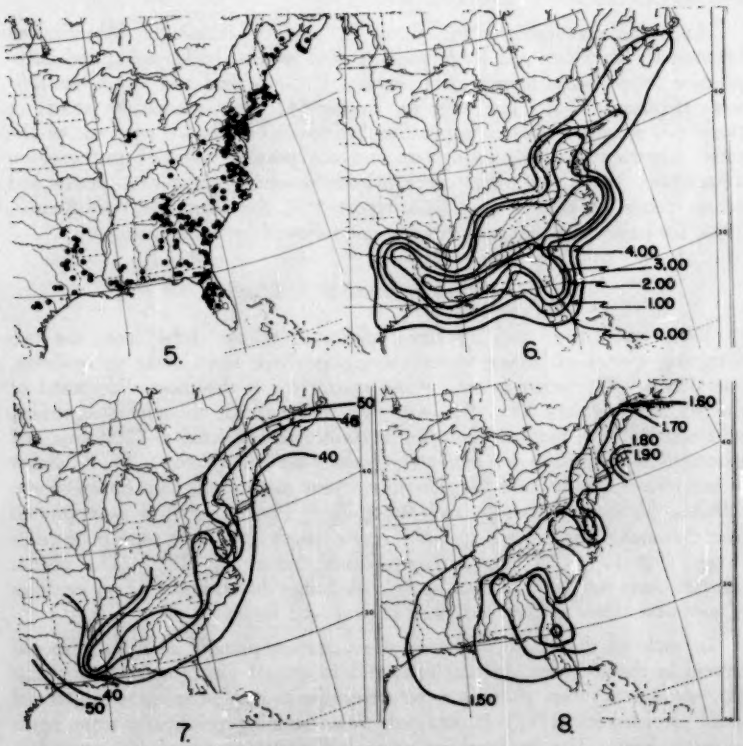
Viola lanceolata subsp. *occidentalis* has not been included in the above discussion because of its geographical isolation and morphological distinctness. A large number of differences were noted between it and *V. lanceolata* subsp. *lanceolata*, though all are quantitative in nature (Russell, 1955). It must

have been isolated from subsp. *lanceolata* since at least the early Pleistocene and perhaps for a much longer period.

VIOLA PRIMULIFOLIA L.

A somewhat similar situation is presented by *V. primulifolia*, a species closely related to *V. lanceolata*. It has been divided into two subspecies, subsp. *primulifolia* in northeastern United States, and subsp. *villosa* (Eaton) N. H. Russell in southeastern and southern United States (fig. 5). The two subspecies differ only in lamina shape and pubescence, and, due to the large range overlap and the presence of many intermediate plants among the specimens examined, no attempt had been made to map the subspecies separately in fig. 5.

Lamina length/breadth ratios have again been used to illustrate lamina shape (fig. 8). A scatter diagram (fig. 13) shows the close correlation



Figs. 5-8.—5. Natural distribution of *V. primulifolia*. 6. Total pubescence values for *V. primulifolia*. A value of 0.00 indicates that the leaf was completely glabrous; of 4.00 that it was moderately pubescent. 7. Lamina length measurements in millimeters for *V. primulifolia*. 8. Lamina length/breadth ratios for *V. primulifolia*.

between these two linear measurements, indicating that size of the leaf does not directly affect its form. The phenocontours for lamina shape (fig. 8) indicate a lack of definite clines for this coastal plain species. A similar situation obtains in lamina length (fig. 7), but in pubescence (Fig. 6) a single center of dispersal is found which extends from Louisiana to Central Georgia. Outward from this narrow region total leaf pubescence diminishes.

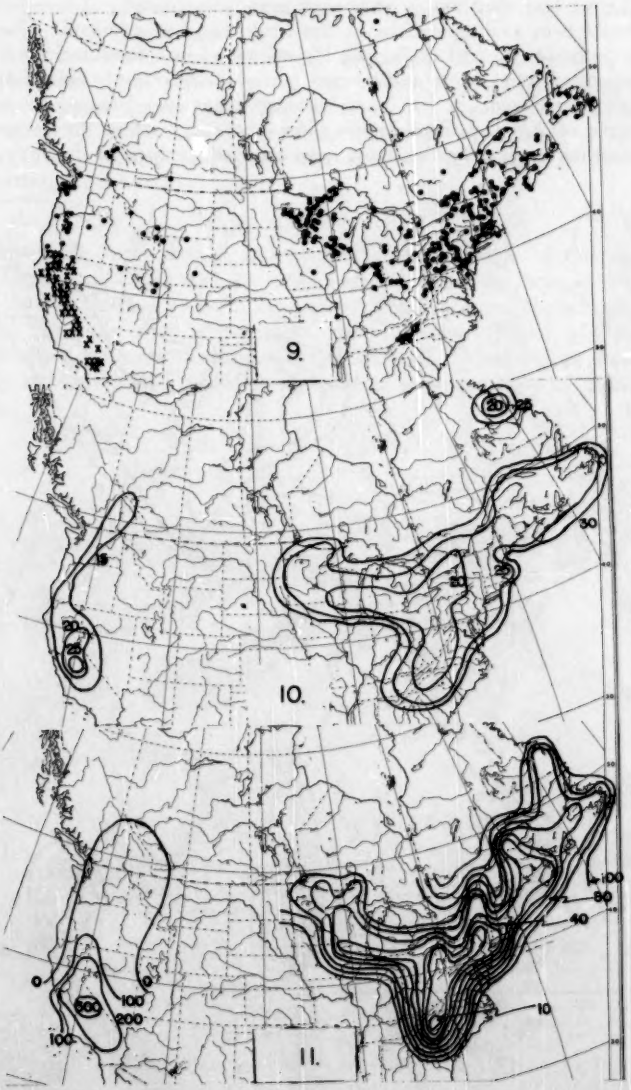
The evolutionary history of the northern and southern subspecies of *V. primulifolia* may be closely similar to that of the eastern subspecies of *V. lanceolata*. However, the two subspecies are much less distinct from each other, and their past separation has probably been neither so long nor so effective. As a result of continued free intercrossing, the two subspecies may be losing their separate identities, and their taxonomic separation may be more an indication of past than of present conditions. On the other hand, the possibility that we are here witnessing the actual specific segregation of two entities cannot be ruled out.

An additional complicating factor is that of occasional hybridization between *V. lanceolata* and *V. primulifolia* and possible backcrossing and introgression. Specimens intermediate between *V. lanceolata* and *V. primulifolia* were frequently seen. For example, among 341 Gray Herbarium sheets of these two species 9 contained putative hybrids. This is 2.6 per cent of the total, a percentage high enough to indicate possible effective introgression (Anderson, 1949). Various other hybrids involving these two species and other species of violets have been reported in the literature (see Russell, 1955, for summary), but are probably not followed by backcrossing.

VIOLA MACLOSKEYI F. E. Lloyd.

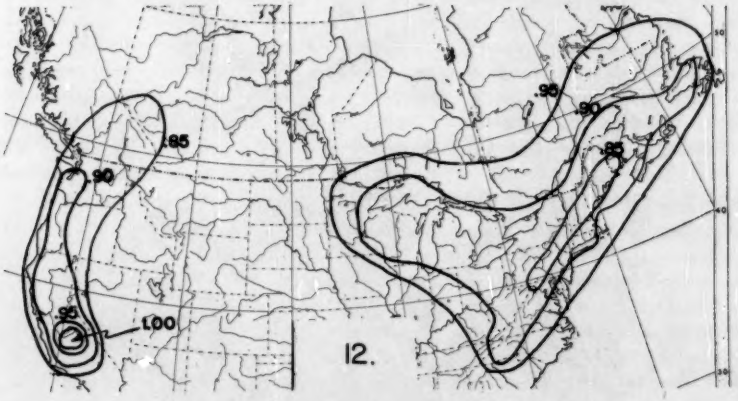
Viola macloskeyi, and the three species to follow, differ from the two foregoing species in having leaves varying in shape from ovate to reniform, but always with cordate bases. *Viola macloskeyi* is the most widespread of the six white violets (fig. 9) with two well-marked, though intergrading, subspecies. *Viola macloskeyi* subsp. *macloskeyi* is restricted to California and western Oregon, while *V. macloskeyi* subsp. *pallens* (Banks) M. S. Baker occurs from Labrador and Newfoundland west to Oregon, with no specimens collected between Minnesota and Wyoming. Three characters were plotted over the entire range of the species: lamina length (fig. 10); total pubescence values (fig. 11); and lamina length/breadth ratio (fig. 12). The phenocontours have not been extended across the range discontinuity as no evidence of east-west clines (across the great plains) was found.

In each of the above instances, the variation pattern indicates dispersal centers in the southern Appalachians and in central California. In the east (*V. macloskeyi* subsp. *pallens*) a picture similar to the "progressive equiformal areas" of Hultén (1937) is obtained, clines running principally from north to south here. The ancestral or original dispersal forms of *V. macloskeyi* subsp. *pallens* are found at relatively high elevations in the southern Appalachians, indicating the use of this area as a refugium during at least the last Pleistocene glaciation.

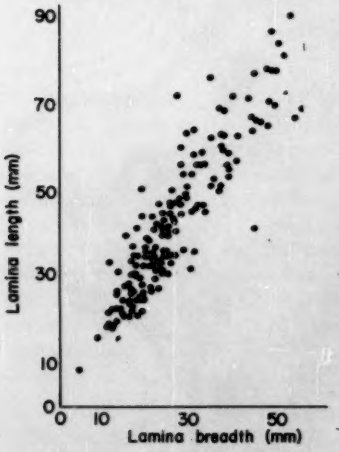


Figs. 9-11.—9. Natural distribution of *V. macloskeyi.* subsp. *macloskeyi* is indicated by the X's, subsp. *pallens* by the dots. 10. Lamina length measurements in millimeters for *V. macloskeyi.* 11. Total pubescence values for *V. macloskeyi.* A value of 0 indicates complete glabrousness; of 300 moderate pubescence.

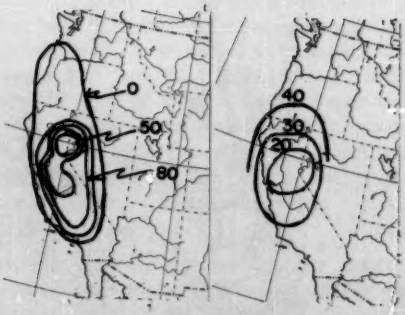
The western situation is somewhat more complicated. There have undoubtedly been two separations in the range of *V. macloskeyi*. The most recent probably occurred during the Pleistocene when a transcontinental range was separated into eastern and western portions. Apparently this disjunction has not been closed. It has been, however, relatively brief, and the western specimens of subsp. *pallens* do not differ appreciably from the eastern. A much earlier range separation must have occurred, perhaps in the early Terti-



12.



13.



14. 15.

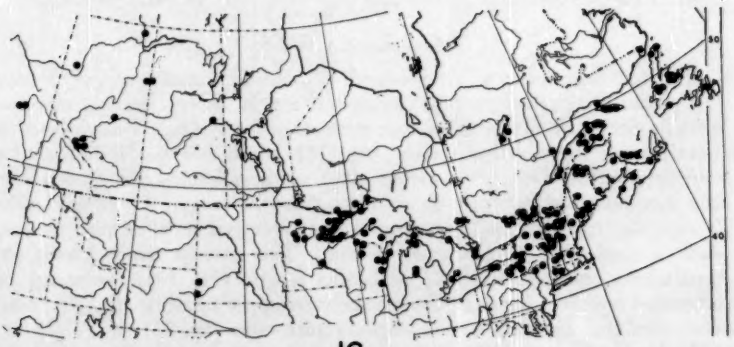
Figs. 12-15.—12. Lamina length/breadth ratios for *V. macloskeyi*. 13. Lamina length plotted against lamina breadth for *V. primulifolia*. 14. Percentage distribution of the pubescence type with laminas hairy on lower surface only (as compared to all other possible types), for *V. macloskeyi* subsp. *macloskeyi*. 15. Number of pairs of crenations per leaf, *V. macloskeyi* subsp. *macloskeyi*.

ary, which could account for the isolation of *V. macloskeyi* subsp. *macloskeyi* in the California mountains.

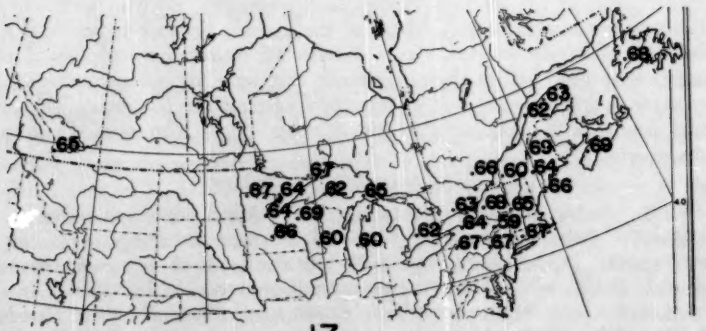
Hybridization and backcrossing are proceeding actively between subsp. *macloskeyi* and subsp. *pallens* on the west coast. Figs. 14 (percentage of a particular type of lamina pubescence—hairs only on the lower surface of the leaf), and 15 (number of pairs of crenations on the leaf blade), in addition to the three preceding figures, illustrate a strong north-south cline due to this continued hybridization.

VIOLA RENIFOLIA Gray.

Perhaps the most distinct and easily the least variable of the stemless white violets is *V. renifolia.* Its range (fig. 16) resembles those of *V. macloskeyi* subsp. *pallens* and *V. incognita.* Though quite distinct morphologically from the other white violets, there is some evidence that it may occasionally hybridize with them in nature (Russell, 1954a). It is characterized by reniform leaves, a lack of vegetative stolons, and no petal beards.



16.



17.

Figs. 16, 17.—16. Natural distribution of *V. renifolia.* 17 Distribution of means for lamina length/breadth ratio of *V. renifolia.*

Though all measured characters (12) were plotted, no clinal variation was found in this species. Little variation of any sort (except in leaf pubescence) was found. In fig. 17 the lamina length/breadth ratio means are listed to indicate the lack of variation and especially the absence of clines. In pubescence, variation from totally glabrous leaves to leaves heavily pubescent in one or more areas was found. This has been considered in a separate paper (Russell, 1954b). Though a variety has been based on a particular type of leaf pubescence, no geographic localization of this or any leaf pubescence type was found, and therefore the variety was considered untenable.

In view of its habitat preference today, *V. renifolia* probably occurred in the higher southern Appalachian mountains and in the fringe of conifer forest before the ice sheets during the late Pleistocene, though today it is no longer present in these areas. Like *V. blanda* (see blow), it is restricted today to a relatively limited geographical area and in this area is infrequent. Its principal affinity with the three preceding species is its chromosome number ($2n = 24$); in most of its morphological characters it is more closely allied to the two following species and may have been ancestral to them.

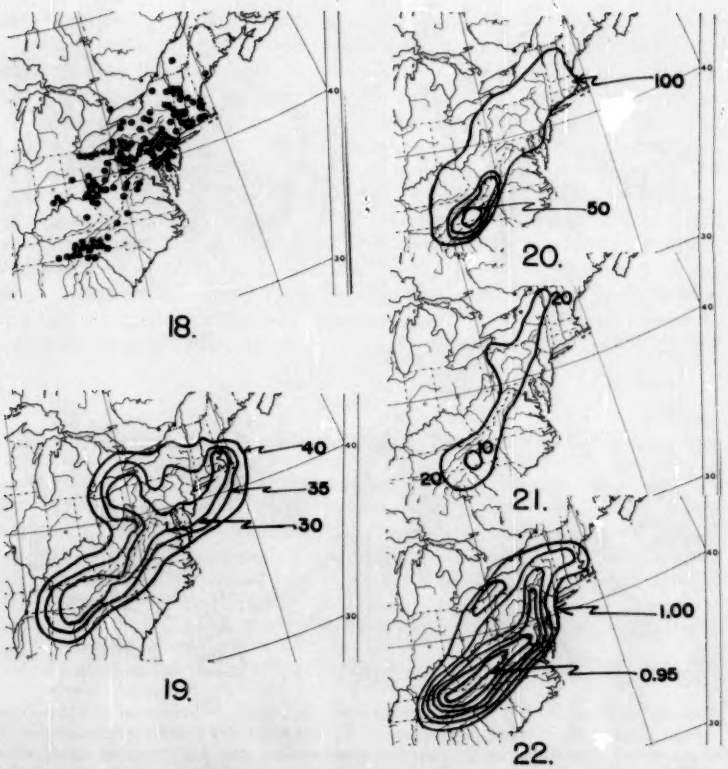
VIOLA BLANDA Willd.

The last two violets to be discussed (*V. blanda* and *V. incognita*) have been placed in the "subgroup" Blandae and are, in several respects, morphologically distinct from the other four stemless white violets. *Viola blanda* is essentially an Appalachian species (fig. 18) which has not spread so far from the Appalachian region as the other white violets. Like *V. renifolia*, little morphological variation occurs throughout its range. However, unlike *V. renifolia*, the variation that does exist is arranged in a definite pattern, which is similar for all characters plotted. This pattern shows a southern Appalachian center in the case of lamina length (fig. 19), percentage of pubescence type one (lamina pubescent only on upper surface) (fig. 20), total pubescence (fig. 21), and lamina length/breadth ratio (fig. 22).

In *V. blanda* as well as *V. macloskeyi* subsp. *pallens*, *V. incognita*, and even *V. primulifolia*, morphologically extreme specimens were found on the higher peaks of the southern Appalachian mountains, often in such localized habitats as mountain bogs. Many of these small, unusual populations must be very effectively isolated. In a number of instances morphological characters were observed on these specimens that were not seen elsewhere. For example, a single specimen of *V. primulifolia* from Roan Mountain, Tennessee, had flowers with sepal auricles several times longer than seen elsewhere in this species.

VIOLA INCOGNITA Brainerd

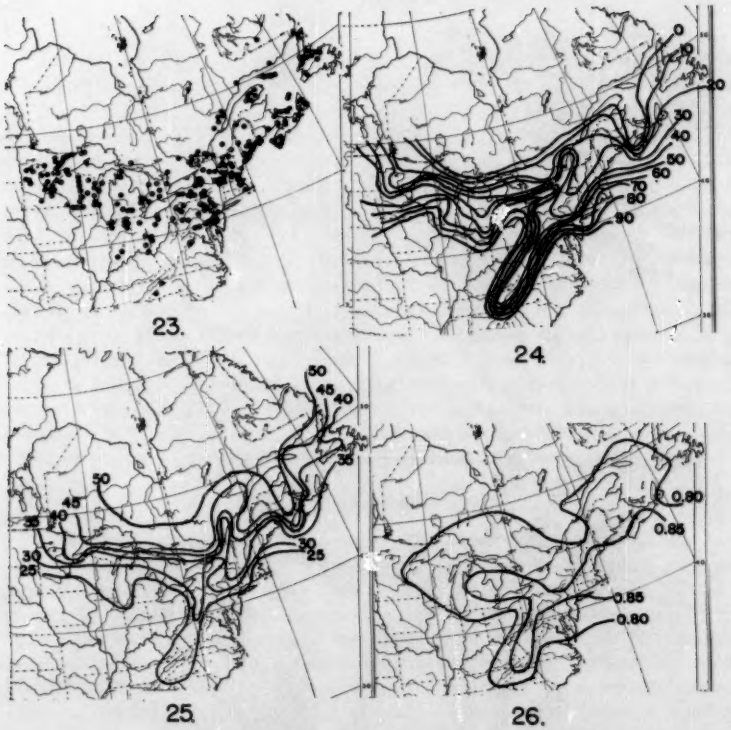
This species is very closely related to *V. blanda*, and specimens are occasionally difficult to classify. No single character always separates the two species, and they must generally be distinguished by combinations of several characters. *Viola incognita*, though occasionally found in the southern Appalachians, is relatively common in conifer and hemlock-hardwood forests throughout the great lake states (fig. 23). Like *V. blanda*, it is a cordate-leaved, stoloniferous violet, but differs in having wider leaves, short, blunt, bearded lateral petals, and often different leaf pubescence



Figs. 18-22.—18. Natural distribution of *V. blanda*. 19. Lamina length measurements in millimeters for *V. blanda*. 20. Percentage distribution of the pubescence type with laminas hairy on upper surface only (as compared to all other possible types) for *V. blanda*. 21. Total pubescence values for *V. blanda*. A value of 10 indicates that the leaf is slightly hairy, of 20 moderately hairy. 22. Lamina length/breath ratios for *V. blanda*.

patterns. In fig. 24, the percentage of lamina pubescence type one (leaves pubescent on the upper surface only) is plotted. The concentration of plants with this type of pubescence increases from north to south, with a tongue extending along the southern Appalachians. This pattern is exactly opposite to that found in *V. blanda* (fig. 20). An index to total pubescence of the leaf (both sides of the lamina, the lamina margin, and the petiole) is given in fig. 25, and indicates that, on the whole, pubescence increases northward. Leaf pubescence is quite complicated in *V. incognita* and *V. renifolia* and has been analyzed at length in a separate paper (Russell, 1954b). In *V. incognita*, as in *V. renifolia*, a variety has been named based on a single pubescence type; this pubescence form was not considered sufficient excuse to maintain an additional taxon.

Lamina shape (fig. 26) is quite variable throughout the range of *V. incog-*



Figs. 23-26.—23. Natural distribution of *V. incognita*. 24. Percentage distribution of the pubescence type with laminas hairy on upper surface only (as compared to all other possible types) for *V. incognita*. 25. Total pubescence values for *V. incognita*. A value of 25 indicates the leaf to be moderately hairy; of 50 to be heavily pubescent. 26. Lamina length/breadth ratios for *V. incognita*.

nita, and only a vague geographical pattern has been found. In the case of leaf shape, as in all other characters examined, morphological overlap with *V. blanda* was frequently found, where the ranges of the two species coincided. The morphological similarity, crossing relationships (Bamford and Gershoy, 1930), ecological relationships, and geographical overlap indicate that *V. incognita* may have been derived from *V. blanda*, perhaps sometime during the Pleistocene. Morphological overlap may be due, therefore, to a lack of complete differentiation. Hybridization is not rare where these species grow together and is often apparently followed by backcrossing and introgression (Russell, 1954a).

SUMMARY

Morphological variation in some leaf characters of six species of stemless white violets was analyzed. In five species clinal variation was demonstrated and found helpful in formulating hypotheses of their recent evolution. In *V. macloskeyi* subsp. *pallens*, *V. blanda*, *V. incognita*, and *V. lanceolata*

subsp. *lanceolata* variation patterns offer some evidence that they occurred in the higher southern Appalachian mountains during Pleistocene glaciations. It is postulated that this region has served as a center of modern dispersal for each of them. *V. renifolia* may have occurred in the Appalachians also, or may have occurred during the Pleistocene in the conifer forest at the edge of the ice. *V. primulifolia* and *V. lanceolata* subsp. *vittata* are both coastal plain violets and undoubtedly spent much of the Pleistocene south of the Appalachian mountains. In the far west, *V. lanceolata* subsp. *occidentalis* probably occurred near the coast, and *V. macloskeyi* subsp. *macloskeyi* in the mountains of southern or central California, later moving out from that region. With the possible exception of *V. incognita*, the actual origins of each of the species cannot be accounted for using only this method of analysis, as they seem to predate the Pleistocene. However, hypotheses have been offered to explain the time and place of origin of their subspecies.

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Notes and Discussion

New County Records of Sedges in Michigan and Indiana

Sedges from Michigan and northern Indiana collected by the writer over a number of years were submitted for determination to Dr. Frederick J. Hermann of the United States Bureau of Plant Industry. Among them the following have been designated by him as "New County Records." Substantiating specimens of all species listed are on file in a separate section of the herbarium of the University of Notre Dame, excepting those from counties followed by the symbol (M). These have been deposited in the herbarium of the University of Michigan. The usual data of labels, such as numbers, dates, stations, habitats, etc., are omitted here, except in the case of new State records or of outstanding range extensions, as superfluous to the purpose of this report, but may be had upon request. Parenthetical annotations are by Dr. Hermann.

New County Records for Michigan

Carex aenea Fern.—Iron Co.
C. alopecoidea Tuckerm.—Huron Co.
C. amphibola var. *turgida* Fern.—Huron Co.
C. angustior Mack.—Ontonagon Co. (M).
C. arctata Boott—Allegan (M), Huron & Iron cos.
C. argyrantha Tuckerm.—Huron Co.
C. aurea Nutt.—Huron, Macomb & Ontonagon cos.
C. backii Boott—Huron Co.
C. bebbii Olney—Arenac (M), Muskegon, Presque Isle & Wayne cos.
C. bicknellii Britt.—Berrien Co.
C. brevior (Dewey) Mack.—Berrien & Huron cos.
C. bromoides Schkuhr.—Cass & Ontonagon cos.
C. brunnescens (Pers.) Poir.—Crawford (M), Huron, Iron, Muskegon, Oakland & Tuscola cos.
C. buxbaumii Wahl.—Berrien, Huron & Iosco (M) cos.
C. canescens var. *disjuncta* Fern.—Berrien, Gogebic, Iron & Tuscola cos.
C. canescens var. *subloliacea* Laestad.—Ontonagon Co. (M).
C. castanea Wahl.—Huron & Ontonagon cos.
C. cephaloidea Dewey.—Huron Co.
C. communis Bailey.—Gogebic (M), Huron (M) & Iron (M) cos.
C. comosa Boott.—Berrien & Huron cos.
C. convoluta Mack.—Huron & Iron cos.
C. crinita Lam.—Crawford, Huron (M), Iron & Ontonagon cos.
C. cristatella Britt.—Berrien & Crawford cos.
C. cryptolepis Mack.—Arenac (M), Huron & Iosco (M) cos.
C. debilis var. *rudgei* Bailey.—Huron Co.
C. deflexa Hornem.—Gogebic Co.
C. deweyana Schwein.—Gogebic & Huron cos.
C. digitalis Willd.—Berrien & Van Buren (M) cos.
C. disperma Dewey.—Gogebic Co.
C. eburnea Boott.—Allegan Co.
C. emmonsii Dewey.—Berrien Co.
C. exilis Dewey.—Mackinac Co.
C. festucacea Schkuhr.—Kalamazoo Co.
C. flava L.—Arenac, Bay & Berrien cos.
C. foenea Willd.—Berrien & Gogebic cos.
C. folliculata L.—Berrien Co.
C. frankii Kunth.—Southwest shore of Hubbard Lake, Alcona Co., No. 1559, July 30, 1950 (Northernmost record); Monroe & Wayne cos. (Previously known only from Kalamazoo Co.)
C. gracilescens Steud.—Berrien Co. (M).
C. gracillima Schwein.—Iron Co.
C. granularis Muhl.—Berrien & Huron cos.
C. grayii Carey.—Huron Co.
C. grayii var. *hispidula* Gray.—Berrien Co.
C. gynandra Schwein.—Swampy woods about two miles north of East Tawas, Iosco Co., No. 4283, Aug. 2, 1954. (Southernmost record.)
C. haleana Olney.—Berrien Co.
C. hirtifolia Mack.—Swampy woodland about two miles east of Iron River, Iron Co., No. 4387, June 13, 1955. Growing with *C. woodii*. (New to northern Michigan; previously not known north of Saginaw Bay.)
C. hyalinolepis Steud.—Monroe Co.
C. incomperta Bickn.—Berrien Co.
C. interior Bailey.—Berrien Co.
C. interior f. *keweenawensis* (Hermann) Fern.—Iron Co.

C. intumescens var. *fernaldii* Bailey.—Ontonagon Co.
C. knieskernii Dewey.—Ontonagon Co.
C. lacustris Willd.—Cass, Gogebic, Iosco (M) & Ontonagon cos.
C. laevivaginata (Kükenth.) Mack.—Berrien Co.
C. lanuginosa Michx.—Berrien & Huron cos.
C. laxiflora Lam.—Huron Co.
C. laxiflora var. *serrulata* Hermann.—Rich slope of river, Thrushwood, Berrien Co., No. 1384, May 26, 1952. (First Michigan record.)
C. leptalea Wahl.—Berrien & Ontonagon (M) cos.
C. leptalea var. *harperi* (Fern.) Stone.—Kent Co. (M).
C. leptonervia Fern.—Allegan, Iron & Ontonagon cos.
C. lupulina Muhl.—Arenac (M) & Sanilac (M) cos.
C. meadii Dewey.—Berrien Co.
C. merritt-fernaldii Mack.—Gogebic Co.
C. molesta Mack.—Berrien Co.
C. normalis Mack.—Berrien Co.
C. oligosperma Michx.—Ontonagon Co.
C. ormostachya Wieg.—Gogebic & Huron cos.
C. pauciflora Lightf.—Van Buren Co. (Southwesternmost record.)
C. paupercula Michx.—Iosco (M) & Iron cos.
C. peckii Howe.—Allegan (M) (Southernmost record) & Huron cos.
C. pedunculata Muhl.—Gogebic Co. (M).
C. pensylvanica Lam.—Berrien, Monroe & Montcalm (M) cos.
C. prairea Dewey.—Berrien Co.
C. projecta Mack.—Crawford, Iron & Roscommon (M) cos.
C. pseudo-cyperus L.—Arenac Co. (M).
C. retrorsa Schwein.—Oakland (M) & Sanilac (M) cos.
C. rostrata Stokes.—Arenac (M) & Berrien cos.
C. rugosperma Mack.—Gogebic, Iron (M) & Ontonagon cos.
C. sartwellii Dewey.—Berrien Co.
C. schweinitzii Dewey.—Alcona Co.
C. scoparia Schkuhr.—Berrien, Crawford (M), Gogebic (M), Huron (M), Oakland & Presque Isle (M) cos.
C. sprengelii Dewey.—Berrien Co.; and very abundant in roadside ditch bordering woods for some 200 yards about two miles east of Iron River, Iron Co., No. 4404, June 13, 1955). (New to northern Michigan; previously not known north of Saginaw Bay.)
C. sterilis Willd.—Berrien & Gogebic (M) cos.
C. stipata Muhl.—Alcona Co. (M).
C. stricta Lam.—Van Buren Co.
C. stricta var. *strictior* (Dewey) Carey.—Huron & Iosco (M) cos.
C. suberecta (Olney) Britt.—Berrien Co.
C. subimpressa Clokey.—Thinly wooded swamp, South Rockwood, Monroe Co., No. 4185, June 28, 1953. (Second record for Michigan.)
C. tenera Dewey.—Berrien, Iron, Oakland & Ontonagon (Northernmost record) cos.
C. tonsa (Fern.) Bickn.—Berrien & Huron cos.
C. tribuloides Wahl.—Chippewa, Huron, Oakland & Tuscola cos.
C. trisperma Dewey.—Arenac & Berrien cos.
C. tuckermani Boott.—Iron Co.
C. vesicaria L.—Ontonagon Co.
C. viridula Michx.—Crawford Co.
C. vulpinoidea Michx.—Alcona (M), Arenac (M), Crawford & Iosco (M) cos.
C. vulpinoidea var. *pycnocephala* Hermann.—Alcona Co.
C. woodii Dewey.—Iron Co. No. 4402. Data as for *C. hirtifolia*. (New to northern Michigan; previously not known north of Saginaw Bay.)

NEW COUNTY RECORDS FOR INDIANA

Carex aggregata Mack.—St. Joseph Co.
C. alopecoidea Tuckerm.—St. Joseph Co.
C. annectens var. *xanthocarpa* (Bickn.) Wieg.—St. Joseph Co. (Second Indiana record.)
C. arctata Boott.—Rich slope south side of lake, Rolling Prairie, LaPorte Co., No. 4214, May 24, 1953. (First substantiated Indiana record.)
C. atherodes Spreng.—St. Joseph Co.
C. bebbii Olney.—St. Joseph Co.
C. bicknellii Britt.—St. Joseph Co.
C. brevior (Dewey) Mack.—St. Joseph Co.
C. conjuncta Boott.—St. Joseph Co. (Northernmost record.)
C. crawei Dewey.—St. Joseph Co.
C. cristatella Mack.—St. Joseph Co.
C. digitalis Willd.—LaPorte Co.
C. emoryi Dewey.—St. Joseph Co.
C. festucacea Schkuhr.—LaPorte & St. Joseph cos.
C. foena Willd.—St. Joseph Co.

C. frankii Kunth.—St. Joseph Co.
C. gracilescens Steud.—St. Joseph Co.
C. gracillima Steud.—St. Joseph Co.
C. gravida var. *lunelliana* (Mack.) Hermann.—St. Joseph Co.
C. hitchcockiana Dewey.—LaPorte Co.
C. interior Bailey.—St. Joseph Co.
C. lacustris Willd.—St. Joseph Co.
C. laxiflora var. *serrulata* Hermann.—LaPorte Co.
C. leptalea var. *harperi* (Fern.) Stone.—St. Joseph Co. (Northernmost Indiana record.)
C. leptonervia Fern.—Woodland, south side of lake, Rolling Prairie, LaPorte Co., No. 4213, May 24, 1953. (First Indiana record.)
C. longii Mack.—St. Joseph Co.
C. mesochorea Mack.—St. Joseph Co.
C. molesta Mack.—St. Joseph Co.
C. muhlenbergii Schkuhr.—St. Joseph Co.
C. rosea Schkuhr.—St. Joseph Co.
C. sartwellii var. *stenorrhyncha* Hermann.—St. Joseph Co.
C. suberecta (Olney) Britt.—St. Joseph Co.
C. tenera Dewey.—St. Joseph Co.
C. tetanica Schkuhr.—St. Joseph Co.
C. texensis (Torr.) Bailey.—St. Joseph Co.
C. trichocarpa Muhl.—St. Joseph Co.
C. vesicaria L.—St. Joseph Co.

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A Grass (Munroa squarrosa) Apparently Cultivated by Ants

On September 18, 1955, while driving through the Painted Desert of Arizona about 18 miles east of Jacob Lake, Conconino County, on our return from a collecting trip for the Plant Introduction Section, we noticed that each of numerous large ant hills scattered over the plain was encircled by a ring of vegetation. Upon examination these rings (about 4 to 6 inches wide) were found in each case to be a pure culture of *Munroa squarrosa* (Nutt.) Torr. Normally this pulvinate-cespitose grass is bright green, but in 1896 Vasey described what he took to be a grayish floccose form of it as "var. *floccuosa*." The fuzz, however, proved to be merely an accumulation of the remains of egg cases of a woolly aphid. The ring of *Munroa* surrounding the ant hills was composed of plants of this type and the ants were busily pasturing aphids upon it. Since the grass seemed to be restricted to the ant hills in this area (although earlier in the day we had found the non-infested green plants to be plentiful along rocky roadsides on the Kaibab Plateau), it had all the appearance of having been deliberately cultivated by the insects, much as certain ants cultivate fungi.

Since we are not conversant with the ways of ants it seemed advisable to consult an entomologist who had given particular attention to the habits of ants in connection with the phenomenon of the grass rings. Consequently our observations were communicated to Professor Neal A. Weber, of Swarthmore College, who replied as follows. "The explanation of this pure culture of grass at this site is probably the fact that the ants were feeding on the seeds of the grass, as these ants are probably the harvesters, *Pogonomyrmex*, and they may frequently tend aphids. It is curious that these and other ants may gnaw seedlings, a habit which [by weeding out other species] may tend to eliminate all but the most abundant plant. Several observers have thought that these harvesters (in North America, Africa and western Asia) bring up from below the stored seeds should they germinate during a wet season. This would account for the ring distribution."

Dr. Marion R. Smith, of the Entomology Research Branch, U. S. Department of Agriculture, referred us to Dr. W. M. Wheeler's account of the Texas harvesting ant, *Pognomyrmex barbatus molefaciens* (Buckl.), in his book "Ants" (Columbia Univ. Press, N.Y. 1910). In this, Wheeler ridicules Lincecum's statement that the Texas harvester actually sows the seeds of the "ant-rice" (*Aristida stricta* and *A. oligantha*) around the periphery of its mounds, and cultivates the crop in addition to harvesting and storing it in its granaries. But there seems to be no reason for assuming, as Wheeler does, that an ant colony would necessarily be entirely dependent for its sustenance upon such a crop if it were cultivated. Nor is his contention that the grass rings are accidental altogether convincing. His own observations of *molefaciens* and its nests revealed that during the

winter the grass seed stored in the ant chambers sometimes sprouts too far to be fit for food and on sunny days the ants may often be seen removing these seedlings and carrying them to the refuse heap at the periphery of mound. Here, he says, the seedlings "often take root and in the spring form an arc or complete circle of growing plants around the nest." Whether, however, he actually saw such seedlings taking root and becoming established is not clear from his account. The probability of plants growing from discarded seedlings that have germinated in the dark is not very great. Such seedlings as a rule are very sensitive to abrupt environmental changes, even a slight change in humidity frequently proving to be lethal. Wheeler comments further that only a small percentage of the nests of the Texas harvester, and only those situated in grassy localities, present such circles. But in the case of the Arizona ant associated with Munroa, neither of these conditions obtained. Here all of the ant hills were encircled by the grass and it was not observed elsewhere in the immediate vicinity where the absence of other green vegetation made the rings particularly noticeable.

Since it appears to be still controversial whether the cultivation of such grasses by ants is accidental or intentional, it is to be hoped that some Arizona biologist, or someone else with ready access to the Painted Desert, may make more detailed observations upon this ant-grass association than we were able to do.—F. J. HERMANN AND B. M. LEESE, Horticultural Crops Research Branch, Agricultural Research Service, U. S. Dept. of Agriculture, Beltsville, Md.

Data on the Heterogonic Growth of the Chela of Some Californian Decapods

The heterogonic growth formula ($y = b \cdot x^k$)[1] has wide application to biology (Huxley, 1932). The constants (b and k) in this formula, for example, may have taxonomic value. For the full realization of this value many more species must be studied as well as a systematic exploration within the taxonomic categories.

During the Summer of 1954, certain common species of decapods were collected. *Hemigrapsus oregonensis* was taken from Point Richmond. *Petrolisthes cinctipes, Hemi-*

TABLE 1.—Values of the constants in the heterogony formula for some decapods.

Species	Sex	Numbers of Animals Collected	k[3]	b (grams)
P. crassipes[4]	Male	60	1.09 1.51	0.17
	Female	40	0.90	0.15
H. oregonensis[5]	Male	56	1.38	0.10
	Female	36	1.07	0.06
H. nudus[4]	Male	53	1.32	0.10
	Female	42	1.09	0.07
P. cinctipes[6]	Male	40	1.28	0.21
	Female	33	1.07	0.19

[1] Where y is the weight of the chela; x is the weight of the body; b is the value of y when x is unity; k is a constant which expresses the ratio between the relative growth rate of the part and the relative growth rate of the rest of the body.

[2] The author wishes to thank Patricia Ortman for her assistance with the collections at Carmel.

[3] Ratio between the growth rate of the right chela and the rest of the body or portion of the remainder as specified below.

[4] In determining k, the weight of the body minus all walking legs was employed.

[5] In determining k, the weight of the body minus both chela was taken.

[6] The weight of the body minus the right chela was used for the determination of k.

grapsus nudus, and *Pachygrapsus crassipes* were obtained from Mission Point, Carmel.[2] It was of interest to know if the differential growth of the chela could be described by the heterogonic growth formula. A search of the available literature failed to reveal data for these species.

The right chela was removed at the breaking-point from formalin-killed crabs. Crabs were separated conveniently into 4 or 5 weight classes for each sex; mean weights for the chela and the body were obtained for each weight class. Mean body weights were plotted along the abscissa of log-log paper and mean chelar weights on the ordinate. The constant b was obtained directly from the graph. The constant k is the value of the tangent of the slope of the line (measured with a protractor).

A single straight line was obtained from these plots except for the case of males of *Pachygrapsus crassipes*, which gave 2 straight lines. These males are not unique (see Huxley for other species showing 2 k values). It may be seen from Table 1 that the values of k and b are larger in males than in females of all species studied. Positive heterogony (k value greater than 1) was obtained for all species except the females of *Pachygrapsus crassipes* which showed negative heterogony (k values less than 1).

SUMMARY

The differential growth of the right chela of four species of decapods collected in this study can be described by means of the heterogonic growth formula. The k and b values are higher in the males than in the females. The larger chela of the male may correlate with the greater importance of the chela in the biology of the male decapod than in that of the female.—ROBERT ORTMAN, University of California, Berkeley.

REFERENCE

HUXLEY, J. S. 1932—Problems of relative growth. London.

Book Reviews

THE GENUS PHLOX. By Edgar T. Wherry. Morris Arboretum Monographs, Philadelphia, Pennsylvania. 1955. 174 pp., 88 figs., 62 maps. $4.00.

In view of the horticultural and botanical importance of the genus Phlox, the lack of a good taxonomic monograph has long been a serious handicap. The difficulties of identification and nomenclature have been felt by horticulturists and botanists alike. With a sense of great satisfaction, therefore, we can greet the appearance of Professor Wherry's well-executed and highly original monograph of Phlox, which represents the summing-up of a life-long study of the genus. Dr. Wherry's small book on Phlox is the only really critical account of the entire genus which has ever been written.

The format is very clear and attractive, for which both the author and the Morris Arboretum of the University of Pennsylvania are to be commended. The lucid descriptions of the 84 taxa grouped into 67 species are accompanied by a beautiful series of photographs taken for the most part in nature and by simple but effective line drawings. The nomenclature is straightened out for each taxon; a short discussion is included in the treatment of each horticulturally important species which ties the confused names applied to cultivars into the botanical system; and common names are proposed for a number of the species, which may or may not be a worthwhile practice. Three species and one subspecies, in addition to several sections and subsections, are described as new, and a large number of new combinations are made in this revision.

The geographical distribution of each taxon is presented in two ways. The limits of distribution are given in degrees and minutes of latitude and longitude; without an atlas at hand one usually does not know what state, let alone what county, is referred to by the description of range. This difficulty is to some extent alleviated by the distribution maps, which show the area of each taxonomic entity superimposed on a political and physical map. Where two or more entities overlap in range, however, and are represented by dots of varying sizes, the range of each taxon is not always easy to see on the map.

No lists of representative specimens are included. In a difficult genus such as Phlox the absence of a definite citation of specimens for each species and subspecies will probably be regretted by many taxonomists.

Not the least valuable feature of *The Genus Phlox* is Professor Wherry's revision of the infrageneric categories. The relationships between certain western and eastern North

American species groups, for example, have not been clear to most botanists. By the composition of his sections and subsections, Dr. Wherry presents his informed viewpoint of the interrelationships within the genus. The picture of natural affinities which emerges from the monograph is in many respects very different from any system proposed in the past.

With regard to the categorical rank applied to the infrageneric groupings, this reviewer would prefer to regard such dissimilar forms as the leafy herbaceous eastern Phloxes and the needle-leaved caespitose woody-based forms of western mountains as belonging in different subgenera rather than in different sections; however, taxonomists are generally agreed that the assignment of these categories to a natural group is a matter of opinion. Some botanists, for example, will disagree with Dr. Wherry as to the exclusion of the reduced Microsteris gracilis group from the genus Phlox; others, including the reviewer, favor this exclusion; but no student of Phlox doubts that a close relationship exists between the two groups.

Dr. Wherry does not present his system of taxonomy of certain highly critical groups of Phlox, such as the caespitose group in the western mountains, as the final definitive statement on the subject. The problems in several groups of Phlox are too complex to be unravelled by field and herbarium studies alone, as Dr. Wherry specifically acknowledges, and he humbly recommends to others the task of working out the many remaining problems by biosystematic methods.

A taxonomic monograph is both the end and the beginning of research. It is itself the product of research; but it also frequently raises as many questions as it answers, and provides the basis for subsequent biological studies, which in the absence of a taxonomic foundation could scarcely be carried out. Perhaps one criterion of the value of a taxonomic monograph is the stimulus and foundation it provides for later biological researches. Judged by this standard, Professor Wherry's *The Genus Phlox* will certainly be a successful work. —VERNE GRANT, Rancho Santa Ana Botanic Garden, Claremont, California.

THE GENUS ACHLYA: MORPHOLOGY AND TAXONOMY. By Terry W. Johnson, Jr. University of Michigan Studies, Scientific Series, Volume XX. The University of Michigan Press, Ann Arbor. xv+180 pages, 22 plates. 1956. $4.50.

This monograph of one of the common genera of water molds represents the first comprehensive review of Achlya since Coker's study of the Saprolegniaceae was published more than thirty years ago. Approximately a third of the species regarded as valid by the author have been described since the appearance of Coker's monograph and about half of this group are also new since the compilation by Coker and Matthews in 1937 in North American Flora. Changes in species included in Coker's monograph are few and amount principally to the reduction of several species to synonymy. The treatment of the species concept follows previous patterns to a large extent, but the organization of the work from a scientific point of view is exceptionally fine, and might well provide a model for others to follow.

An 18-page introduction includes a characterization of the genus and a historical review, together with brief but entirely adequate description of methods employed in collection, cultivation and examination of material. The introduction concludes with definitions of taxonomic criteria and terminology. An accompanying plate serves to illustrate the descriptive terms quite clearly. This introduction is followed by a systematic account of the genus, subgenera and species. The taxa are in three groups depending upon whether they are regarded as valid, of doubtful affinities, or excluded from the genus. In all cases in which living cultures were studied the localities and the collectors are cited, or if the material examined was preserved it is so stated. It is thus made quite clear just how much direct evidence the author has for his concept of each taxon. Another separate paragraph lists recorded collections with references to the bibliography. Each description of the valid taxa concludes with a discussion by the author. The one exception that might be taken to the treatment of the group is the inclusion of two unnamed species in the section devoted to valid taxa of the same genus. These are listed by the author as *Achlya sp.* 2. Since the author felt that they required further study before naming, it might have been more logical to place them in the section devoted to taxa of doubtful affinity.

Exceptionally clear and well composed plates of drawings are provided of all valid taxa, with the exception of two, which the author had not seen.—JOHN A. JUMP, University of Notre Dame, Notre Dame, Indiana.

AUTHOR INDEX

SUBJECT INDEX

NOTE—Names of new genera, species, indicated by italics.

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